The Effect of Spatial and Environmental Drivers on Patterns in Species Richness and Composition

Dissertation zur Erlangung des akademischen Grades Dr. rer. nat.

vorgelegt der Fakultät für Biologie, Chemie und Geowissenschaften
der Universität Bayreuth

von Herrn Manuel Jonas Steinbauer (M.Sc. Global Change Ecology)
geboren am 14.07.1983 in Geisenhofen

Die vorliegende Arbeit wurde in der Zeit von 06/2009 bis 06/2013 in Bayreuth am Lehrstuhl für Biogeografie unter Betreuung von Herrn Prof. Dr. Carl Beierkuhnlein angefertigt.

Vollständiger Abdruck der von der Fakultät für Biologie, Chemie und Geowissenschaften der Universität Bayreuth genehmigten Dissertation zur Erlangung des akademischen Grades eines Doktors der Naturwissenschaften (Dr. rer. nat.).

Dissertation eingereicht: 05.06.2013

Zulassung durch die Prüfungskommission: 11.06.2013

Wissenschaftliches Kolloquium: 24.09.2013

Amtierende Dekanin: Prof. Dr. Beate Lohnert

Prüfungsausschuss:
Prof. Dr. C. Beierkuhnlein
Prof. Dr. H. Feldhaar
Prof. Dr. Th. Köllner
Prof. Dr. E. Beck
PD Dr. G. Aas

Contents:

1. Introduction

1.1. Motivation

All ecological communities are characterised by a certain degree of diversity (Olszewski 2004) and complex interactions among components operating on different spatial and temporal scales (Storch & Gaston 2004; Steinbauer 2009). One of the fundamental goals of ecology is the identification and understanding of general patterns or regularities that emerge on specific scales or might even be scale-independent (Rosenzweig 1995). The importance for this task originates from the scientific desire to gain knowledge as well as from the impossibility to protect biotic diversity at all levels of organisation (Sarkar & Margules 2002). Decision making and prioritization in the use of biotic resources and in nature conservation are necessarily based on (not always direct) observations or measurements.

A detection and quantification of diversity patterns and a deeper understanding of the underlying causes can thus not only enhance the quality of decisions for nature conservation and the use of natural resources, but also positively influence the aims of these decisions by increasing knowledge on - and awareness for the biosphere. However, most decisions are made unconsciously and motivation rarely originates only from necessity. *"No one could work on the mechanics of diversity without being fascinated by it for its own sake"* (Rosenzweig 1995).

1.2. Structure of this thesis

My thesis starts with examining the general underlying processes that generate patterns in species diversity. It subsequently introduces important general patterns of species richness or species composition and discusses the current knowledge on causes and interactions. This part includes findings from the eight manuscripts of this dissertation. Those are thereafter shortly summarised and my contribution to them is clarified. Based on that I show gaps in current knowledge and I develop novel research hypotheses. While the frame for this thesis addresses diversity patterns in general, a strong emphasis is put on island biogeography. A large part of the knowledge on drivers and patterns of species diversity patterns originates from this research field. In addition, most manuscripts of my thesis use data from islands or other isolated systems. Species diversity research is a melting pot of different ecological sub-disciplines and often suffers from imprecise terminology and definitions. Selected concepts and terms that I considered to be especially vague or very important are therefore discussed and defined separately (Box 1).

Please enjoy reading and be free to contact me in case of questions, criticism and collaboration ideas.

Box 1: *Definitions and explanations for some important, disputable or vague concepts and terms. As nearly all ecological disciplines contribute to species diversity research and theory, terminology is often vague, imprecise or not at all defined and used with different meanings. Especially the use of "physical" terms is disputable (process, mechanism etc.) as the associated concepts in ecology never have the precision and repeatability that are expected for its proper meaning. However, it lies beyond the scope of this work to provide a comprehensive novel frame for definitions and nomenclature in ecology. Clarifications are only provided if necessary for understanding and terminology is else used as commonly done in ecology and related disciplines.*

Carrying capacity: Within the frame of species diversity theory, *carrying capacity* refers to the overall number of species a site under focus would be able to host. Note that the term is used differently in population ecology were it refers to the overall number of individuals a population can support in a specific site. Ecologists are generally aware that communities are no distinct units (Whittaker 1967), but models and theory implicitly refer to the assumption of closed systems. Ricklefs (2006a) suggests that "*flexible filling of niche space was too complicated to be handled by theory*". A limited *carrying capacity* of certain areas or a limit of resources that either constrains the number of species or individuals (also *saturation* in Ricklefs 2006a) is implicitly assumed by a number of concepts including *the metabolic theory of ecology* (Chapter 1.4.4.; Brown et al. 2004) and current island biogeographical concepts (Chapter 1.4.7.; Whittaker et al. 2007, 2008, 2010). Gehrke & Linder (2011) highlight the difficulty to distinguish between *carrying capacity* and *diversification* when investigating drivers for species richness. *Carrying capacity* is suggested to be limited by resource availability and other environmental properties and thus changing with time (e.g. ontogeny of an island) (Whittaker et al. 2007, 2008, 2010). As the same resources may, however, be used by different species, species interactions are suggested to limit coexistence (Emerson & Kolm 2005). A restricted *carrying capacity* is often associated to *niche space* or *niche packing* (see below) and especially accepted for "local" sites (Ricklefs 2010).

Diversification: The diversification rate is commonly defined to result from the rate of speciation and extinction (e.g. Emerson & Kolm 2005; Manuscript 2). It is thus defined as the rate of change in diversity (Futuyma 2009). Similar to "rates" of speciation the interpretation and measurement of "diversification rate" varies depending on the research question. Diversification rate may denote the net change of species numbers *per area* or *per species*. If normalised to a "rate per species", it is interpreted the likelihood of a species to split or vanish in a given time. In most cases a differentiation among the meanings is not necessary, but for certain questions it is crucial (e.g. effect of species richness on diversification rate*)*.

Ecological niche and niche space: The persistent occurrence of a species is influenced by environmental conditions (Grinnellian niche concept, Grinnell 1908, 1917) as well as by biotic interactions (stressed in the Eltonian niche concept; Elton 1927). A niche as used here describes the biotic and abiotic factors that enable a species to persist. Individuals are not expected to reproduce and thus populations to persist outside the niche (Hutchinson 1957; Holt 2009; Wiens et al. 2010). The niche is said to be defined by a set of organismic traits, which may change rapidly but tend to be very conservative. Even while not mentioned in literature, behaviour and especially generation transferred information (culture), which exist among animals (Verzijden et al. 2012), is part of those traits. Additionally, Ricklefs (2010) distinguishes between population and individual niche space. Traditionally the niche is defined based on the distribution, resource utilisation, and function performed by a species either including species interaction (Eltonian niche) or not (Grinnellian niche) (see Soberón 2007). While the niche usually is defined based on spatial occurrence of species, the temporal niche (Levin 2006) finds much less consideration. Here, I follow Holt (2009) and Wiens et al. (2010) by using the niche as an abstract concept that integrates all species'traits interacting with environment and with other biota.
It is assumed that the maximum number of species that a local site can support is defined by specific environmental and biotic properties (see *carrying capacity*). By using environmental resources and interacting with other biota, species are imagined to "occupy ecological space" that is referred to as "niche space" (Ricklefs 2010). This idea is still very prominent and especially local saturation of species richness widely accepted (see Chapter 1.4.3. & 1.4.4.), despite the fact that it is proven that the number of species that can be supported by similar environmental settings or available resources, are strongly controlled by the qualities of species involved and subject to evolutionary processes (Loreau 2000). An increased specialisation of species with time may e.g. increase the number of species that can be supported by the same environmental setting (Svenning 2001). Ricklefs (2010) highlights that despite of this niche space as well as species richness appear to be relatively stable over long periods of time.

Ecological processes, mechanism and repeatability: The meaning of terms varies among scientific disciplines, as does the context of scientific practise. In ecology, experiments can never be repeated precisely, as not all environmental influences can be controlled for. This is especially the case as biota have a specific history that influences their behaviour or reaction on environmental changes (Walter et al. 2012). Nonetheless, general tendencies,

correlations or events and reactions can be distilled from repeated exposure or observations. From this knowledge general "mechanisms" (explanations for the creation of a phenomenon, subject or object) and "processes" (events of transformation) may be identified. However, all causalities are to be seen in the frame (spatial and temporal scale, history) of the observed systems. A common assumption is that the relation between likelihood and environmental/spatial factors does not change in time more than our observation error.

***Equilibrium**:* MacArthur & Wilson (1963, 1967) equilibrium model of island biogeography suggest species richness on an island to be the net balance between species that colonise and disappear from the island. Heaney (2000) more recently introduced aspects of tri-variate equilibrium of colonisation, extinction and speciation. In fact a number of models and studies are based on this assumption (Chen & He 2009; Rosindell & Phillimore 2011). However, especially for remote islands it is generally accepted that a simple model predicting species richness of an island as the static result of the three fundamental processes is not profound enough as the environmental and biotic context for speciation, colonisation and extinction is changing constantly (Heaney 2000).

***Rate of colonisation, extinction or speciation**:* Within the seminal model of island biogeography MacArthur & Wilson (1963, 1967) considered the "rate" of colonisation and extinction to be the number of species being gained or lost on a focal unit (mainly an island) for a given period of time. Especially in phylogenetic studies dealing with evolution, speciation rate is, however, often used as the average time one species takes, under given circumstances, to split into two sister species (e.g. Knope et al. 2012; see also Yule 1924). Under an assumption of neutrality (all species have equal speciation rates), both approaches are tightly related. However, a precise assessment becomes very complicated when studying either the relation between speciation and area (the focal unit or anything correlated with it) or the relation between speciation and species richness (or anything correlated with it like the number of habitats). This is the case as a change in the "rate" can mean two different things. It can either denote an altered chance of the single species to evolutionary radiate. Or it can mean that more species radiate at the same time for a given area. In order to disentangle this problem I differentiate "rate per species" or "rate per area" if necessary. Please see Manuscript 5 for problems arising from undifferentiated usage of the related terms. Further differentiations may be needed under particular circumstances. For example, the process of colonisation includes the establishment of a species. It may be debatable if a species is established after perennial occurrence, first successful reproduction or after reaching a "*stable"* population size. For speciation "*transition time*" or "*time for speciation*" is sometimes differentiated from *"local speciation intervals"* (Coyne & Orr 2004; Futuyma 2009). While the first one measures the time one species needs from reproductive isolation to the formation of a new species, the second term refers to the average time that is needed from one species evolution until this species splits again into two species branches**.**

1.3. Development and maintenance of species richness and composition

1.3.1. Correlations and causes of diversity

The multitude and diversity of organisms is immense. In fact, traits like organismic body mass span across more orders of magnitude, from small microorganisms (10^{-13}g) to large plant species (10^{8}g), than the scale differences between the earth and the entire galaxy (West & Brown 2005). Despite the known constraints of the taxonomic system, the classification of biota into species has been accepted as the primary system of categorisation of life on earth (see Steinbauer 2009). Species richness integrates the occurrences of different species at a specific area and varies widely over spatial scales. The question of the origin of diversity in species and the reason for its pattern is one of the oldest and most fundamental in ecology reaching not only back to the times of Alexander von Humboldt and Alfred Wallace but was likely already in the interest of early human hunters and gatherers (Lomolino 2001). An understanding of underling processes is not only an inherent scientific goal but also considered a prerequisite if we ever want to be able to predict ecological response to environmental changes (White et al. 2010; Guisan & Rahbek 2011), a task that might be partly impossible due to the complexity and inherent non-continuities of living systems.

Species are adapted to specific ecological niches and their occurrence is influenced by interspecific interaction and local environmental circumstances (Hutchinson 1957). However, historical signals (from various temporal scales) are also reflected in current species distributions (Beck et al. 2012). Causal drivers for a now observed pattern might have a time lag that can range back decades (Aggemyr & Cousins 2012) or even millions of years (Kissling et al.

2012). Thus the origin and maintenance of site-specific species richness and composition is recognised to be the result of local environmental settings, historic properties of biota and the environment (Ricklefs 2004, 2006a).

A multitude of interacting drivers are influencing the occurrence of a focal species at a specific location. However, the presence or absence of a species is always the result of three fundamental processes, namely colonisation, extinction and speciation (MacArthur & Wilson 1967; Ricklefs 2004; Wiens et al. 2007). All three processes are tightly linked to spatial and environmental filters (Figure 1; Table 1), making it non trivial to differentiate their effect on species richness and composition. Understanding these filters and their complex interactions is crucial when studying species diversity. In addition, the strength and nature of underlying drivers for species diversity patterns may be strongly scale dependent (Evans et al. 2008).

Especially due to improved data availability and computational progress, research is currently very successful in the identification of general diversity patterns especially on large spatial scales (see recent success of the ecological discipline "Macroecology"). However, there is still a deficit in identifying causalities and processes that are ultimately underlying those patterns (Beck et al. 2012). Environmental factors correlated to species richness must be related to the three fundamental processes in order to advance theory (Wiens et al. 2007). The aim to identify the processes responsible for an emerging pattern in diversity is part of the identity of biogeography and ecology (West & Brown 2005). In fact it is claimed that "*any satisfactory explanation of diversity must be rooted in those rates* [colonisation, extinction and speciation]" (Rosenzweig 1995).

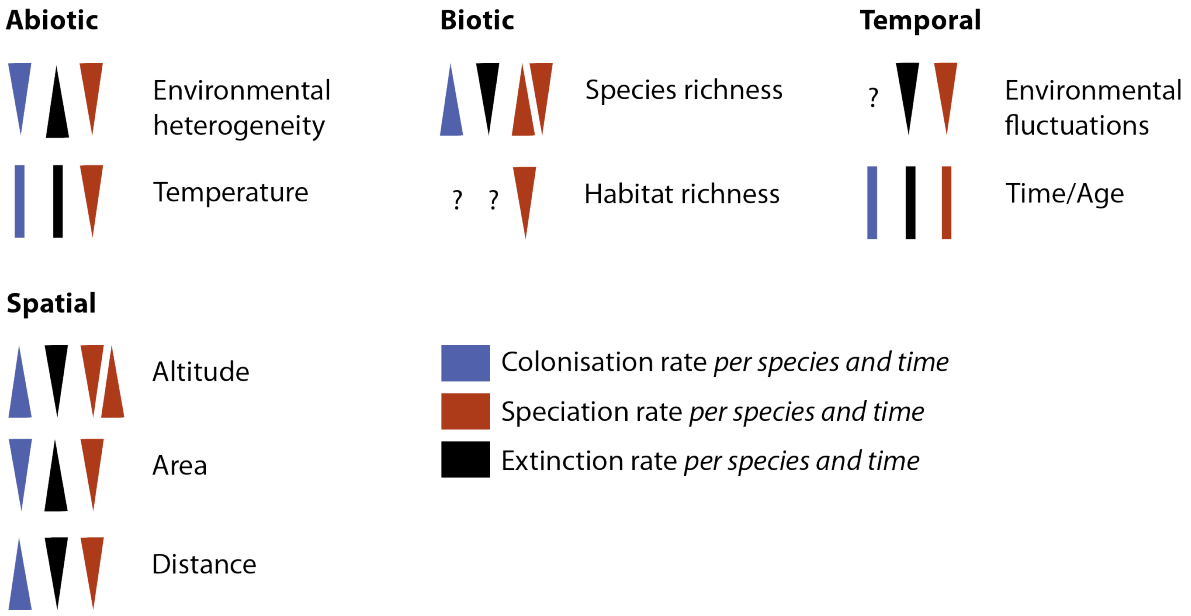

Figure 1: Theories on the relative effect of ecological variables on the rates per species of extinction, speciation and colonisation is indicated by triangles with higher rates at the bold side. Please refer to Table 1 for related hypotheses, literature and scientific acceptance of the relation. Note that opposing effects might be postulated in the literature (Table 1).

Islands exhibit defined isolated parts of the complex environmental macrocosm and are thus the best places to study the fundamental processes colonisation, extinction and speciation (MacArthur & Wilson 1967). The first comprehensive theory addressing the effect of environmental and spatial filters on species diversity patterns originates from island biogeography (MacArthur & Wilson 1963, 1967). While the equilibrium theory of oceanic island biogeography postulated a dynamic equilibrium of species richness on an island in dependence of the opposing effects of colonisation and extinction, novel models especially incorporated evolutionary aspects and the geomorphological ontogeny of islands with time (Whittaker et al. 2008).

Table 1: Comprehensive overview on some suggested mechanisms, applied proxies and associated theory and literature for the three fundamental processes of colonisation, extinction and speciation. The "general acceptance" reflects my own perception from reading the literature.

	Mechanism	**Indicator**	**Related hypotheses and theories**	**Further prominent references/ related chapters**	**General acceptance**
Colonisation rate per species	Isolation	Distance (geographic, environmental or functional)	- *Theory of island biogeography* (MacArthur & Wilson 1967)	Heaney (2000); Chapter 1.3.2.	Generally accepted
		Elevation	- *Elevation-driven ecological isolation* (Manuscript 2)	MacArthur (1972); Chapter 1.5.	First proofs within this thesis
		Area	- *Target area effect* (Whitehead & Jones 1969).	Chapter 1.3.2.	Generally accepted
	Community resistance (inter- and intraspecific competitive exclusion)	Species richness, number of individuals, species similarity	- *High density blocking* (Hewitt & Ibrahim (2001)	Waters (2011); Chapter 1.3.2.	Generally accepted
		Species traits	- *Priority effects* (Urban & De Meester 2009) - *Competative exclusion (*Waters 2011)	Waters (2011); Chapter 1.3.2.	Generally accepted
		Time of colonisation			
	Phylogenetic similarity	Phylogenetic history	- *Phylogenetic niche conservatism*	Wiens & Donoghue (2004); Chapter 1.3.2. & 1.4.4.	Generally accepted
	Local niche differentiation/ coexistence	Environmental/ resource heterogeneity	- *Resource heterogeneity hypothesis* (Hutchinson 1959; Huston & De Angelis 1994)	Gundale et al. (2011); Chapter 1.3.2. & 1.4.3.	Generally accepted
	Species filtering	Regional species availability/ pool		Tscharntke et al. (2012); Chapter 1.3.2.	Generally accepted
	Unclear (niche space available)	Habitat diversity (area, elevation), Species richness, Environment		Triantis et al. (2012b); Chapter 1.3.2.	Unclear
	Carrying capacity		- *Diversifiction is hindered by diversity* (Ricklefs 2010)	Chapter 1.3.2.	Often claimed in theory but not proven
	Larger species pool, historic climate	Temperature	- *Tropical niche conservatism hypothesis (Wiens & Donoghue 2004)*	Kalmar & Currie (2007); Chapter 1.4.4.	Speculation

	Mechanism	Indicator	Related hypotheses and theories	Further prominent references/ related chapters	General acceptance
Extinction rate per species	Isolation	Distance (geographic, environmental or functional)	- *Rescue effect* (Brown & Kodric-Brown 1977)	Sutherland et al. (2012); Chapter 1.3.3.	Generally accepted
			- *Climate change extinctions*		
		Elevation	- *Via Area and isolation* (MacArthur 1972)	Manuscript 2, 3 & 5; Chapter 1.5.	Accepted but not proven
	Population size				
		Available energy, productivity	- *More individuals hypothesis* (Wright 1983)	Evans et al. (2008); Beck et al. (2011); Chapter 1.3.3. & 1.4.4.	Generally accepted
		Area	(MacArthur 1972)	Rosindell & Phillimore (2011); Kisel et al. (2011); Chapter 1.4.3.	Generally accepted
	Small island effect		- *Island extinction risk* (Lomolino & Weiser 2001; Ricklefs 2012)	Triantis et al. (2012a); Chapter 1.3.3. & 1.4.3.	Causes under debate
	Species interactions	Species richness, density or individuals, environment, Community size	- *Diversity begets diversity* (Emerson & Kolm 2005)	Ricklefs (2006a); Carnicer et al. (2007, 2012); Chapter 1.3.3.	Speculation, under debate
	Carrying capacity		- *Diversification hindered by diversity* (Ricklefs 2010)		
	Paleoclimatic refugia	Distance to paleoclimatic refugia		Hortal et al. (2011)	Speculation
	Change in environment	Environmental stability with time	Wallace (1878)		Generally accepted
	Genetic diversity		- *Founder effects* (Stuessy et al. 2012; Habel & Zachos 2012)		Generally accepted
Speciation rate per species	Isolation	Distance (geographic, environmental or functional)	- *Theory of island biogeogra-phy* (MacArthur & Wilson 1967)	Heaney (2000); Rosindell & Phillimore (2011); Chapter 1.3.4.	Generally accepted
		Elevation	- *Elevation-driven ecological isolation* (Manuscript 2)	Manuscript 3 & 5; Chapter 1.3.4. & 1.5.	First proofs within this thesis
		Area	- *Intraspecific gene flow* (Kisel & Barraclough (2010)	Rosindell & Phillimore (2011); Kisel et al. (2011); Chapter 1.3.4.	Strong indications
	"Opportunity for divergence"		- *Area thresholds* (Losos & Schluter 2000; Lomolino 2000b)		
	Time available	Time (age)	- *Time for speciation effect (*Stephens & Wiens 2003)	Ricklefs (2006a); Chapter 1.4.7.	Generally accepted, no effect on rate per species
	Unclear (niche space available)	Habitat richness, Elevation, topographic heterogeneity	- *Opportunity for divergence* (Stuessy et al. 2006; Triantis et al. 2012b, Knope et al. 2012)	Losos & Schluter (2000); Manuscript 5; Chapter 1.4.6.	Claimed but not proven; Lack of con-sistent theory
	Carrying capacity	Species richness, environment	- *Diversifiction is hindered by diversity* (Ricklefs 2010)		Claimed but not proven
	Local differentiation	Environmental heterogeneity	- *Small-scale genetic differentia-tion* (Svenning 2001)	Halas et al. (2005); Manuscript 5; Chapter 1.4.6.	Unclear
	Temporal rhythms	Land use, temporal variabil-ity, disturbances	- *Temporal niche* (Jentsch et al. 2011)	Chapter 1.4.7.	Unclear
	Temperature	Temperature, latitude, elevation	- *Metabolic theory of ecology*	Qian & Ricklefs (2011); Kalmar & Currie (2007); Chapter 1.4.4.	Unverified assumption, hot debate
	Species interactions	Species richness or species density	- *Diversity begets diversity* (Emerson & Kolm 2005)	Manuscript 2; Chapter 1.3.4.	Speculation

1.3.2. Colonisation

The investigation of colonisation rate was especially triggered after MacArthur & Wilson (1963,1967) introduced the equilibrium theory of island biogeography that proposes islands species richness to be the result from a balance of colonisation and extinction of species. Within the model, colonisation is mainly constrained via *isolation by distance* (MacArthur & Wilson 1963, 1967). Geographic distance is, however, just a correlate for the likelihood of transportation or dispersal. The geographical setting of possible vectors and filters and the mode and intensity of transport of the species in focus is a more direct influential factor. Thus anything that alters the chance of arrival or establishment of species is considered to influence the colonisation rate like e.g. the area of the focal island (*target area effect;* Whitehead & Jones 1969) and dispersal limitations (Franklin et al. 2012).

It is suggested that dispersal ability affects species turnover and accordingly also richness across spatial scales (Lenoir et al. 2012). Dispersal ability often changes with the live stage of individuals (Sutherland et al. 2012). Limited dispersal capacity is a major driver for the species distribution pattern in those European landscapes that exhibit a remarkable postglacial colonisation lag (Schneeweiss & Schönwetter 2010; Essl et al. 2011; Dullinger et al. 2012). Especially high mountain chains have been shown to be effective dispersal barriers and species with a wider elevational distribution range tend to be faster in post-glacial re-colonisation (Dullinger et al. 2012). Dispersal limitations by mountain chains with east-west orientation as well as the Mediterranean Sea have hindered latitudinal range shifts of species following climatic changes. This is one of the main causes for the overall lower species richness in Central and Northern Europe in comparison to comparable latitudes in America or Asia (Svenning & Skov 2007).

Species composition on islands usually represents a "*dispersive*" subset of species present on the mainland (Whittaker & Fernández-Palacios 2007). Over long distances dispersal is usually associated with non-standard ways of transportation (Higgins et al. 2003) and is said to be highly stochastic (Lewis 2000; Clark et al. 2001). Causal drivers for long-distance dispersal are difficult to proof and even more challenging to quantify. They might e.g. include transportation via large storm systems (Monzón-Argüello et al. 2012) or secondary dispersal, e.g. via predators of seed dispersing birds or lizards, which is expected to be a common mode of transport (Nogales et al. 2012).

However, the dispersal filter is only the first barrier a colonising species needs to overcome. In addition, differences in environmental features between source and sink region reduce the likelihood of successful establishment (Manuscript 2, 3 & 5). In less isolated systems, establishment seems to be even more difficult than crossing the dispersal filter (Carlquist 1966). Unfortunately, dispersal or transfer and establishment abilities are often correlated to the same physical features which makes a detailed assessment challenging (Dennis et al. 2012). The process of colonisation integrates both, successful dispersal or transport and establishment. Establishment (but also secondary arrival of individuals of an already present species) may not only be hindered via environmental constraints or non-adjusted temporal (e.g. seasonal) rhythms. It may also be prevented via inter- (and intra-) specific interactions like neutral demographic processes ("*high density blocking*" sensu Hewitt & Ibrahim 2001) or *competitive exclusion* (Waters 2011). The importance of biotic interactions in establishing populations is additionally highlighted by a number of examples where the extinction of one species was followed by colonisation success of another that was beforehand excluded via competition (Waters 2011). The most prominent example is the penguin *Megadyptes antipodes*. It successfully colonised mainland New Zealand only few hundred years after its relative *Megadyptes waitaha* went extinct (Lopes & Boessenkool 2010).

The first colonisation of oceanic islands occurs within years to decades, presumably due to lacking competition (Thornton et al. 1988). Subsequently, the rate of successful colonisers slows down with time (Whittaker et al. 2008). Priority effects ("first come first serve"; Lomolino

2000a) may define future colonisation patterns (the first species hinders the second one from establishing even if the second one would be more competitive once established; e.g. Urban & De Meester 2009; Mergeay et al. 2011). In fact, the influence of species interactions on large-scale species distribution is uncertain, but priority effects probably influence current species distribution on various scales (Waters 2011; Dullinger et al. 2012).

Besides their isolation, islands are in most cases more limited in environmental resources in terms of quantity as well as heterogeneity than continental areas (Dennis et al. 2012). High-elevation ecosystems on islands or mountains are special cases constituting islands within islands. Environmental filtering along the elevational gradient and the small area of high-elevation zones makes colonisation here much less likely than in low elevations (Manuscript 2). Within this thesis, I demonstrated that isolation of ecosystems on islands or mountains tends to increase with elevation, as source ecosystems with similar environmental settings are farther apart and smaller in area (Manuscript 2 & 5, Chapter 1.5.1.). This has ample implications including an increase in diversification (see Box 1) and thus in the percentage of endemics with elevation (but see Manuscript 2 for discussion). The identification of endemic hot spots in high elevations raised considerable public interest (e.g. Cordis News 2012). Further theoretical implications are discussed in Chapter 1.5.2.

1.3.3. Extinction

Extinction is much less understood than colonisation and speciation. One reason is, that the absence of once present species is in retrospective difficult to trace, especially on large time scales. In addition, natural occurring extinctions are superimposed and often masked by the overwhelming numbers of human induced species losses (Sekercioglu et al. 2004). Especially on islands, first human colonisations were mostly followed by a rapid change in vegetation often including a shift in dominant tree species and a spread of grasses, shrubs and exotic species as well as a change in fire regime (Connor et al. 2012). Fossil records and pollen analyses can provide a hint on changes in species composition (de Nascimento et al. 2009) or the introduction of invasive species (Zöller et al. 2003, 2004) in the past.

The model of island biogeography (MacArthur & Wilson 1963, 1967) assumes an equal chance of extinction for each species on an island. A larger species richness results consequently in a higher number of species that go extinct per time. However, there are also claims that the probability of extinction *per species* (see Box 1) increases with diversity due to more intense species interactions and thus stronger selection pressure (Emerson & Kolm 2005). As the increased competition is also supporting speciation, diversification is suggested to increase despite the higher rate in extinctions (*Diversity begets diversity* hypothesis, Emerson & Kolm 2005; but see Manuscript 2). An upper limit of diversity in any location, however, needs to be caused by a decline in diversification (see Box 1) with species richness (Ricklefs 2010, 2006a). In fact, a constant absolute or relative species limit of a specific area is assumed in many theoretical models including the metabolic theory of ecology (Brown et al. 2004; Gillooly et al. 2004) and the present general model of island biogeography (Whittaker et al. 2007, 2008). While not entirely understood, it is supposed that (close to) saturation conditions are reached in most ecological systems on earth (Ricklefs 2010).

Area, which is correlated with species richness (Chapter 1.4.3.), has a direct effect on extinction rate *per species* by sustaining larger populations and more heterogeneous environmental conditions that buffers fluctuations in the physical environment (e.g. in climate; MacArthur & Wilson 1967; Whittaker et al. 2008). In case of small areas, a local extinction of sub-populations may be hindered by the constant inflow of individuals from other areas (r*escue effect;* Brown & Kodric-Brown 1977). Thus dispersal capacities and connectivity of the matrix are decreasing the likelihood of local extinctions. Dispersal and migration ability is also important in case of large-scale climate fluctuation. In Europe, dispersal barriers have caused the extinc-

tion of a large number of species during ice age fluctuations (Svenning & Skov 2007), while some have survived in regional climate refugia (Médail & Diadema 2009).

Recent models combining evolutionary plasticity and dispersal ability have shown that a larger dispersal capacity of species may also increase the overall numbers of extinctions by negative species interactions in case of climate change (Norberg et al. 2012). In general, co-evolutionary dynamics and species interactions are seen as important correlates for species extinctions besides extrinsic drivers (Ricklefs 2006 a,b).

1.3.4. Speciation

One prerequisite for speciation, the splitting of one species in two or more sister species, is reproduction barriers and limited gene flow (often caused by isolation; Heaney 2000; Rosindell & Phillimore 2011 but also possible via other mechanisms) as well as time (*time for speciation effect*; Stephens & Wiens 2003). The total number of species on an island decreases as isolation increases, but this relation often levels off for islands under extreme isolation where speciation is the dominant way of species gain (MacArthur & Wilson 1963,1967; Rosindell & Phillimore 2011). Neutral stochastic processes are too slow to explain species diversity patterns that evolved via speciation or colonisation (Ricklefs 2012). Average time between speciation events differ remarkably between organism groups, studies and disciplines. Palaeontological (Sepkoski 1998) and phylogenetic (McPeek & Brown 2007) studies estimate 0.01 to 10 speciation instances per million year and lineage, while the rate of speciation in isolated systems may be between 40 and 40,000 times higher than that (Rosenblum et al. 2012 and references therein). Some authors like Carroll et al. (2007) suggest that these high rates of diversification may be more common than previously thought. One explanation is that rapid speciation is a common phenomenon, but that new evolved species are very susceptible to extinctions and nearly never persist over longer time scales (Rosenblum et al. 2012). Especially on oceanic islands, new arriving species initially tend to show a very high rate in diversification, which declines with time (Givnish 2010).

However, early arriving species do not always show high rates of speciation and adaptive radiation (Givnish 2010). Temporally alternating transitions from colonisation periods and time of adaptive radiation were suggested by Wilson (1959,1961) in the famous theoretical framework on "taxon cycles" (Ricklefs & Bermingham 2002). In addition to that, several authors have highlighted that clades typically show a limited period of rapid evolutionary dynamics early in their existence (Ricklefs 2010 and references therein). In general, random drift and "*nearly neutral*" processes (Presgraves 2010) are too slow to account for the observed temporal turnover of species. Other external (climate and environment) as well as internal drivers (interactions) need to influence speciation (Ricklefs 2006b). Especially the availability of "opportunities" or "empty niche space" has been suggested as one driving force for rapid speciation (Ricklefs 2010). Ricklefs (2010) assumes that "niche space" is relatively constant over longer time periods and an increase in species richness should thus, to his opinion, be self-limiting with a feedback on speciation and extinction. Diversification of some clades must thus be balanced by shrinkage of others (Ricklefs 2010). This theory is in contrast to the suggestion that intensified interactions enhance species selection and adaptation and with that trigger speciation (*Diversity begets diversification* hypothesis; Emerson & Kolm 2005; but see Manuscript 2).

Rapid speciation is considered to take place if one species manages to adapt to a new environment (overcome niche conservatism; Wiens et al. 2010). The evolution of novel traits boosts diversification (Carnicer et al. 2012). Especially limited dispersal and gene flow initiates genetic differentiation and increases speciation rate (Givnish 2010). In general, faster growing plants with a shorter life cycle have higher speciation rates than large, long-lived species (Givnish 2010 and references therein). In addition, "compensated trait loss" is a common phenomenon in coevolution (Ellers et al. 2012). In this case, the loss of one trait is compen-

sated by a mutualistic interaction with another species. This phenomenon is especially relevant for genetic divergence of sister populations (e.g. island - mainland), where in one population trait loss is compensated and thus supported by a mutualistic partner that is not present in the other population.

Speciation is suggested to increase with area, with larger areas especially supporting cladogenesis (Rosindell & Phillimore 2011). Stuessy et al. (2006) highlights that adaptive radiation increases with island area, elevation and habitat diversity (i.e. the number of vegetation units) with all three variables being highly correlated (see Chapter 1.4.6. & 1.5.). Area-thresholds have been identified after which the species-area relation (Chapter 1.4.3.) is steeper. On islands of the Caribbean exceeding 3000 km^2, speciation in lizards has even been shown to exceed extinction rates resulting in a net increase of species numbers (Losos & Schluter 2000). In addition species-area curves only for endemic species are steeper than those for the total number of specie (Rosindell & Phillimore 2011). Manuscript 2 supports this view by illustrating a positive correlation between historic habitat area and the degree of endemism. Lomolino (2000b) even suggests that a minimum area needs to be reached to enable speciation. However, the reasons for the positive relation between area and speciation are still unclear. Obviously, increased species turnover on small islands hinders speciation due to a lack of species persistence (*time for speciation effect*; Stephens & Wiens 2003, Chapter 1.4.7.). However, the positive *speciation-area effect* remains even when the effect of different aged islands is considered in the analyses (Losos & Schluter 2000). Possibly, an increase of habitat diversity with area supports speciation due to effects discussed in the frame of available "niche space" (Stuessy et al. 2006; see Chapter 1.4.6. and Manuscript 5).

Topographic heterogeneity tends to increase differentiation in climatic niches and thus increase speciation (Schnitzler et al. 2012). However, a number of cases where islands with higher habitat diversity have lower (or no) species evolved via speciation compared to large islands with lower habitat diversity are in contrast to this assumption (Losos & Schluter 2000). Again, area is correlated with island elevation, which increases isolation for high-elevation ecosystems (Manuscript 2 & 5), a hypothesis supported by the fact that many endemic lizards of the Caribbean are adapted to specific elevational ranges (Losos & Schluter 2000). Development of theories is hindered by the correlation among variables and the imprecise use of terminology in the context of habitat heterogeneity (see Chapter 1.4.6. and Manuscript 5). Losos & Schluter (2000) for instance claim, "*Puerto Rico is a very old island with great vegetational and topographic diversity, yet it has experienced many fewer speciation events than Hispaniola and Cuba*". Puerto Rico (1338 m), however, also reaches a much lower elevation than Cuba (1974 m) and Hispaniola (3097 m). Thus, while a positive speciation-area relationship becomes commonly accepted (e.g. Givnish 2010), all proofs refer to examples where area, elevation and some measures of habitat diversity are not clearly differentiated (Losos & Schluter 2000; Stuessy et al. 2006; Kisel & Barraclough 2010). In addition, there seems to remain an imprecise use of speciation rate as *number of species an area gains per given time* and number of species as lineages gain per given time (see Box 1). Thus, the widely recognised *speciation-area relation* should remain cause of debate and interest of study (see Chapter 1.4.3.).

1.4. Patterns in species richness and composition

1.4.1. Paradigms, discrepancies and scale dependence

Species differ in their ability to respond to variation in their environment and species diversity thus varies along environmental gradients (Lomolino 2001). The detection of underlying causal mechanisms for biotic patterns is influenced by grain of the observation and size of the study area (Rosenzweig 1995; Beierkuhnlein 2007, Evans et al. 2008; Manuscript 1). In addition, local species richness and composition is not only determined by environmental properties. It is to a large degree dependent on a regional species pool and demographic dynamics (Carnicer et

al. 2012; Lenoir et al. 2012; Tscharntke et al. 2012). However, studies on the effect of local to regional richness (and vice versa) provide contrasting results (Sfenthourakis & Panitsa 2012). A high variability in species composition among samples of different time points makes assessments additionally challenging (Adler et al. 2005). Despite that, ecologists have identified patterns in species diversity that are remarkably constant with scale. Species richness - the most often investigated property of species assemblages (Whittaker et al. 2001) - is known to be mainly correlated to proxies for energy, heterogeneity, disturbances and history with a large influence of scale and stochasticity (Guisan & Rahbek 2011). However, correlation reflects not necessarily causality and explanations for those patterns are often interrelated.

In the following paragraphs I provide an overview on the most prominent patterns of species richness and composition, elaborate suggested causal mechanisms and provide some hints on interactions among these patterns and explanations (summarised in Table 1). Even if not all explanations are equally convincing, they should be discussed because they can hardly be tested with available data sets. Only few hypotheses on species diversity have ever been clearly rejected (Ricklefs 2012 and references therein). Note that already Palmer (1994) lists more than 200 hypotheses on species diversity patterns, indicating the overall complexity and diversity of the topic.

Most of the explanations for species diversity patterns assume some degree of neutrality that is to say species are expected to be equal in their response to changes in the environmental context, or that existing differences level out on the large scale. Of course, neither species nor individuals are really equal (Dall et al. 2012). However, treating them neutral in certain questions may support our holistic understanding of ecological systems. An increase of area, for instance, will likely always increase the number of individuals present of any species.

Human impact has altered the patterns of nature to an extent where an unbiased study is hardly possible. As an example, the number of plant species on oceanic islands has (despite extinctions) approximately doubled since human contact due to introduced species (Sax et al. 2002). However, human impact has also caused a multitude of research opportunities by altering ecosystems and initiating semi-natural experiments. This dissertation follows the tendency of other scholars to ignore or account for human impact on diversity gradients as long as reasonable and possible, as the primary focus of the work is on natural processes. However, especially Manuscript 8 directly addresses the effect of human alteration on species composition or dominance structure.

In recent years, mathematical models have provided increasing knowledge on species diversity patterns. Especially field ecologists tend to be suspicious whether those models really help in understanding biogeographical patterns. Nevertheless, those models summaries and formalise the current knowledge and check its implications. A lack of accuracy thus often indicates a lack in the general understanding of the processes that shape natural patterns.

1.4.2. The distance-decay relationship

The concept that environmental conditions vary non-randomly and that spatially close sites tend to be more similar must have been familiar to early human hunters and gatherers (Lomolino 2001). In fact an increasing dissimilarity with distance is observed within a multitude of systems not restricted to biological systems (Nekola & Brown 2007). In ecology the phenomenon was studies quite early (Whittaker 1960, 1972; Preston 1962), but was increasingly investigated after a publication of Nekola & White (1999). Similarity is commonly assessed by comparing the composition of species assemblages of two localities (Jurasinski et al. 2009). It is primarily investigated in a spatial context (*distance-decay*, Soininen et al. 2007), but temporal similarity (*time-decay, temporal turnover*) is increasingly recognised in literature (Korhonen et al. 2010; Soininen 2010; Kreyling et al. 2011; Stegen et al. 2012).

The spatial species turnover is seen as a primary cause of the species-area relationship (Chapter 1.4.3.), and was also suspected to be one cause of the latitudinal diversity gradient (Chase 2010; Kraft et al. 2011; see Chapter 1.4.4.). On a global scale geographical distance accounts more to the explanation of similarity patterns in species composition than environmental differences (Qian & Ricklefs 2012). It is found in nearly all systems including temperate (Jentsch et al. 2012; Schmiedinger et al. 2012) and subtropical landscapes (Uddin et al. 2011) as well as among oceanic islands (Manuscript 3). The decline in similarity of species composition with geographic distance is commonly traced back to spatial environmental gradients (Nekola & White 1999; Tuomisto et al. 2003) including local disturbances that initiate regime shifts (Bel et al. 2012). In addition, properties of the landscape filter transport of individuals or diaspores (Garcillán & Ezcurra 2003). However, dispersal constrains may be induced by space or species properties alone (Hubbell 2001; Soininen et al. 2007). Even a change in the importance of stochastic processes (e.g. priority effects, sampling) or temporal species turnover along spatial gradients may initiate a decline in community similarity with distance (Stegen et al. 2012).

When investigating species similarity gradients, species turnover can be separated into two components, species replacement (i.e. one species in an assemblage being replaced by another) and species nestedness (i.e. species richness differences; inverse of species replacement), respectively (Almeida-Neto et al. 2008; Baselga 2010; Carvalho et al. 2012). A precise differentiation between both aspects and in particular the definition of nestedness remains controversial (see Almeida-Neto et al. 2008; Schmera & Podani 2011; Ulrich & Almeida-Neto 2012).

Studies on distance-decay are especially prominent in high impact journals and in tropical systems (Condit et al. 2002; Duivenvoorden et al. 2002; Ruokolainen & Tuomisto 2002; Tuomisto et al. 2003; Green et al. 2004). It is therefore surprising that a systematic assessment of the influence of sampling design on the phenomenon was missing so far, despite the fact that scale dependence of species richness patterns is a widely known phenomenon (e.g. Arrhenius 1921; Palmer & White 1994; Beierkuhnlein 1998; Lira-Noriega et al. 2007; Dengler et al. 2009).

By using a simulation-based assessment of distance-decay I could show that the current methodologies commonly used to assess distance-decay are strongly influenced by grain and extent of the sampling procedure. Especially comparisons among different studies (e.g. Jones et al. 2006, Duque et al. 2009; Lenoir et al. 2010) as well the use of different sized sampling units (e.g. La Sorte et al. 2008; Fattorini 2010; Winter et al. 2010; Manuscript 3) are not appropriate (Manuscript 1).

1.4.3. Species-area relationship

Distinct patterns of diversity can be observed on various spatial and temporal scales. However, there are only few patterns that are claimed to emerge at a multitude or at all scales. The most prominent example for species richness is the *species-area relationship*. An increase in species richness with sampling area was mentioned in 1777 (Forster 1777) and quantified in 1835 (Watson 1835). However, it was the publications of Arrhenius (1920, 1921) and Gleason (1922) that stimulates consistent ecological research until today (e.g.Triantis et al. 2012a). Still the power model suggested by Arrhenius is considered as the best approximation of the relationship of species richness and area (Connor & McCoy 1979; Triantis et al. 2012a).

However, the debate regarding the right statistical relation remains unsettled (Tjørve 2009). Uncertainties remain especially towards the upper end of the distribution (very large areas; existence of an asymptote; Williamson et al. 2001; Lomolino 2002) and towards the lower end (very small units; "*small island effect*"; Lomolino 2000b) as well as in respect to data sampling (Scheiner et al. 2011). The slope of the regression line is generally accepted to vary with the

scale of observation (Rosenzweig 1995).

Area is considered to be a surrogate for different ecological drivers (e.g. energy, habitat types, elevation range and age range; see Triantis et al. 2008b and references therein) often associated with the available "*ecological space*" (sensu Gillespie 2006) or "*carrying capacity*" (sensu Triantis et al. 2008b) that limits the capacity of an area to host species. The ecological niche for many species is not directly defined by abiotic conditions but in most cases also by biotic interactions. "*Ecological space*" thus summarises the multitude of environmental influences as well as biotic conditions (Triantis et al. 2012a), both of which may have changed with time and are thus dependent on evolutionary history. In recent years, joint approaches assessing the effect of time and area simultaneously have become particularly popular (Scheiner et al. 2011). Especially in island biogeography the perspective changes towards a process oriented view, where area directly (*target area effect*, Whitehead & Jones 1969; *rescue effect*, Brown & Kodric-Brown 1977) or indirectly (via *carrying capacity*, Whittaker et al. 2008) affects colonisation and extinction dynamics (Lomolino 2000b, see Chapter 1.3.2. & 1.3.3.). Additionally, a suspected increase in speciation rate *per species* with area should enhance the species-area relationship (Lomolino 2000b; Losos & Schluter 2000; Kisel & Barraclough 2010; Kisel et al. 2011; see Chapter 1.3.4. for critical remarks).

When the units of focus are subsamples of larger entities, spatial turnover in species composition is considered to be the main driving factor for an increase of species richness with area (Chapter 1.4.3.). Thus all causes that initiate spatial turnover in species composition may also cause a species area relationship. This includes filtering of species along environmental gradients (Tuomisto et al. 2003) and landscape heterogeneity (Garcillán & Ezcurra 2003) but also a change in the temporal species turnover with space (Stegen et al. 2012).

The relationship of species richness with area differs among species groups. On islands, for instance, species-area curves are reported to be steeper for endemic species than for recent colonists or all species (Triantis et al. 2008a). The general species-area relationship was fundamental for the development of many ecological theories including the theory of island biogeography (MacArthur & Wilson 1963,1967). Relevant for the next chapters is its confirmation on island archipelagos (Manuscript 2, 3 & 4) and the theoretical implication of a decline in species richness with elevation (see Manuscript 2 & 5, Chapter 1.5.).

1.4.4. Latitudinal diversity gradient

The latitudinal diversity gradient, a decline of species richness with increasing latitude, is consistently observed across taxonomic groups, space, scale and habitat (Hillebrand 2004). Its consistency in time is arguable (Mittelbach et al. 2007; Mannion et al. 2012). Higher species richness in the tropics in comparison to temperate regions has already been reported by Darwin (1859) and Wallace (1878) and is considered to be one of the most comprehensively documented patterns in ecology (Kraft et al. 2011). However, the causes for the decline in species richness with latitude are still under debate (Qian & Ricklefs 2011; Giehl & Jarenkow 2012). It has especially been stressed that high correlations are, especially in this context, not necessarily associated to causality (Mittelbach et al. 2007).

A variety of different causes for the latitudinal diversity gradient have been proposed ranging from environmental stability or predictability over productivity, habitat heterogeneity, habitat diversity, area to aridity, seasonality or temperature (Rohde 1992). Initially it has been suggested that the larger area and the time with climatic stability of tropical in comparison to temperate regions enabled a larger diversification in tropical ecosystems (Wallace 1878). Support for the area hypothesis comes from paleoecology, where Mesozoic dinosaur richness does not peak in the tropics but in mid-latitudes where the largest landmasses existed (Mannion et al. 2012).

A long-time span available for evolutionary processes in the tropics is suggested to increase specialisation and species interactions as well as coevolution (Schemske et al. 2009, see *time-diversity relationship* in Chapter 1.4.7.). In addition, long-term stability might induce a lower tolerance of tropical species in respect to environmental fluctuations (Janzen 1967). Both mechanisms highlight the higher specialisation of tropical species in comparison to species of higher latitudes. An increase in species' range size with increasing latitude is a well-known phenomenon (*Rapoport's rule*, Stevens 1989 based on findings of Rapoport 1982). A small spatial and environmental range causes a high change of species' populations to become genetically isolated in case of spatially scattered suitable environmental conditions. This enhanced genetic isolation supports higher rates of speciation of low latitude species in comparison to species of higher latitudes (Salisbury et al. 2012). However, hypotheses associated to long-term stability are challenged by the fact that the climate of tropical systems underwent considerable fluctuations (Mittelbach et al. 2007).

Alternatively it is suggested that not necessarily climatic stability but climatic similarity of current tropical climates to past global climates might be the causal explanation for the current pattern in species diversity (see *paleoclimatic influences,* Chapter 1.4.7.). Tropical tree species richness is highly correlated to the time-integrated area covering a specific climate back to the Eocene (Fine & Ree 2006). Given the – on the time scale of million years – long term cooling trend on earth, most lineages have evolved under climatic condition more similar to tropical than to temperate systems, which may be a primary cause for lower species richness in higher latitudes (*tropical niche conservatism hypothesis*; Wiens & Donoghue 2004). Niche conservatism predicts that areas with environmentally different conditions compared to those under which most lineages have evolved will host less species as closer related species also tend to have similar environmental niches (Wiens et al. 2010). One fact supporting this idea is the finding that temperate taxa are often nested within tropical ones and less often vice versa (Mittelbach et al. 2007). Lineages along the tropical-subtropical transition zone are more often restricted to one of them than predicted by chance (Giehl & Jarenkow 2012). In addition, many flowering plant lineages originate from and diversified in the extensive tropics of the early Tertiary (Davis et al. 2005). Thus niche conservatism hinders a colonisation of temperate climates by tropical taxa (and vice versa). The fact that more species face their climatic limits with drier and colder conditions is also known as the "*physiological-tolerance hypothesis*" (Currie et al. 2004), which is in its essence close to niche conservatism. However, there remain severe inconsistencies, as species do not fill all climatically suitable areas in equal manner (Currie et al. 2004).

The high correlation between latitude and temperature has led to suggestions of causality in the context of the metabolic theory of ecology (Rohde 1992). Already in 1805 Willdenow stated, "*the warmer the climate the greater [...] the number of growing plants...*" (Lomolino 2001). Generally, species richness increases with temperature and water availability (Francis & Currie 2003). Summer temperature is e.g. the best correlate for species richness across different spatial grains in British birds (Evans et al. 2008). The metabolic theory of ecology not only aims at explaining the latitudinal diversity gradient but also intends to provide a conceptual framework for ecology, even if prominent patterns like the species-area (Chapter 1.4.3.) and species-time relationship (Chapter 1.4.7.) remain unaffected (Gillooly et al. 2004). Its key assumption is that the metabolic rate, as nearly all rates of biological activity, increases with temperature (Gillooly et al. 2004). The relation of the metabolic rate to temperature influences a multitude of biotic processes ultimately also reflected in diversity patterns. The metabolic rate measures the rate at which individuals gain, loose and transform energy. For heterotrophs the metabolic rate is directly related to respiration, while it is related to photosynthesis for autotrophs (Gillooly et al. 2004). There are several concepts how a higher temperature may result in larger species richness of a specific site. First, energy availability is expected to increase the abundance of individuals (i.e. through higher productivity) buffering them from extinctions and in consequence increase the number of species per area (*more-individuals*

hypothesis; Wright 1983 in Evans et al. 2008). However, even if there is evidence for a positive relation between abundance and species richness for some species groups (Beck et al. 2011), there is evidence that this chain of argumentation does not hold in general (Currie et al. 2004).

Furthermore, it is suggested that small and warm species have a fast ecological turnover and thus also rapid evolutionary dynamics. This results in higher speciation rates in comparison to larger and less warm biota (Gillooly et al. 2004). This increase of speciation rate with temperature is also a core assumption of the "*speciation rate hypothesis*", which postulates a varying speciation rate with climate. This variation can either be directly caused by faster speciation rates or by stronger interactions under warmer conditions, respectively. Tests of the speciation rate hypotheses are few and results are inconsistent (Currie et al. 2004; Allen & Gillooly 2006). Davies et al. (2004) identified an independent contribution of temperature on mutation rate and species richness in tropical regions.

The idea that species richness is largely the result of species interactions and coevolution is known as the "*Red Queen*" phenomenon (Van Valen 1973) and more intense interactions are especially thought to increase selective processes and extinction (Gillooly et al. 2004, Emerson & Kolm 2005; see also *diversity begets diversification* Chapter 1.3.4.). Functional diversity increases towards the equator and is, on the regional scale, in the tropics even higher than expected from species richness (Swenson et al. 2012). This fact supports an influence of interactions on species richness and not vice versa.

Implicitly, the metabolic theory of ecology assumes a limited carrying capacity (Box 1) of certain areas or a limit of resources that either constrains the number of species or individuals (Brown et al. 2004; Gillooly et al. 2004). This however, would result in a decline in speciation or colonisation or an increase in extinction as soon as carrying capacity is met. As organisms actively or passively alter the resource and element composition of their environment the constancy of carrying capacity can, if at all, not be absolute.

An entirely different suggestion for causality of the latitudinal diversity gradient is an increase in species turnover with energy availability (e.g. Evans et al. 2008). However, this increased local beta diversity in tropical systems as underlying cause for species richness has recently proven to be unlikely. Higher beta diversity in the tropics can directly be explained by the higher regional gamma diversity (Kraft et al. 2011).

1.4.5. Elevational diversity gradients

Elevational gradients in species richness are often seen as a complementary, replicable alternative to studies of the latitudinal diversity gradient (Lomolino 2001; Sanders & Rahbek 2012). They provide ample opportunities for ecological research. Fundamental insights of ecology like the niche concepts (Grinnell 1917) or community composition gradients (Whittaker 1967) originating from observations along elevational gradients (McCain 2009; Sanders & Rahbek 2012). As mountains cover one quarter of the earth surface, Körner (2007) stresses the importance to clarify the role of altitude in the ecological context to "*advance the altitude-related theory of life*". Even if a negative relation between species richness and elevation was assumed until the 1990s, it is now generally accepted that in most cases species richness shows a hump shaped relation with elevation (McCain 2009; Karger et al. 2011).

Elevation is, however, an indirect variable correlated to other factors that in fact influence the species diversity pattern (Austin 2002; Alexander et al. 2011). Suggested causes include the species-area relationship (e.g. Rosenzweig 1995, see Chapter 1.4.3.), where the declining area with elevation negatively affects overall species richness and the mid domain effect (Colwell et al. 2004 and references therein; Alexander et al. 2011), where species' elevational distribution ranges overlap at mid elevations leading to an accumulation of species there. In addition, current climatic conditions are suggested to affect the distribution of species along elevation.

Here similar causes are discussed as for the latitude-diversity gradient (Chapter 1.4.4.). First, warmer areas are in general suggested to support speciation processes (*metabolic theory of ecology*; Rohde 1992). Second, following the theory associated to *niche conservatism* (Chapter 1.3.4. & 1.4.4.) most species also in temperate systems originate from tropical lineages and should thus be adapted to warmer and wetter conditions (Mittelbach et al. 2007). McCain (2007, 2009) suggests that this would lead to higher species richness in mid elevations in dry mountains as species occurrence is limited by drought conditions in low elevations and by water availability in high elevations. Reasons for the low water availability in high altitudes include the fast runoff due to deep slopes and bare rocks and low water retention capacities of often missing or thin soils as well as the temporal water inaccessibility due to frost conditions. This decline in water availability should also decreases species richness in wet mountaintops were drought should not affect species richness in low elevations (McCain 2009). On oceanic islands, high elevation ecosystems face an additional shortage of water due to low precipitation above the trade wind invasion layer (Manuscript 8). Finally, recent studies especially stress negative but also positive effects of species interactions on the altitudinal distribution of species (Anthelme & Dangles 2012; le Roux et al. 2012) altering diversity patterns in complex ways.

In general even clear correlations of species richness with environmental variables may originate from quite complex relationships (Pau et al. 2012). No single mechanism can be detected to be responsible for the current diversity gradient along altitude (Sanders & Rahbek 2012). A general decline of colonisation rate with elevation has been proposed due to environmental filtering along the elevational abiotic gradient (Lomolino 2001; Manuscript 2). Especially the time of first colonisation has been shown to affect current clade species richness (Wiens et al. 2007).

However, McCain (2009) highlights a lack of knowledge in our understanding of speciation and extinction along elevational gradients. He hypothetically suggests maximum speciation and minimum extinction in low elevations but acknowledges the fact that these theories are not tested due to a lack of suitable methodologies and data such as time calibrated phylogenetic trees. Within this thesis this research gap could partly be filled by the application of a novel indicator for speciation processes (Manuscript 2, 3 & 5) showing that empirical data hint towards the opposite of McCain's suggestions. Chapter 1.5. provides details and further implycations of my findings.

1.4.6. Heterogeneity diversity relationship

Heterogeneity in the environment is considered to be one of the most important correlates with species diversity (Tilman & Pacala 1993; Tamme et al. 2010; Douda et al. 2012). However, the multitude of proposed definitions and mechanisms is commonly pooled in an imprecise aggregation of ideas and perceptions. Palmer (1994), who mentions more than 120 hypotheses on species richness claims, "*habitat diversity, environmental heterogeneity, and spatial variability are essentially equivalent*". Even "*habitat diversity*" and "*habitat heterogeneity*" are commonly used as synonyms (Palmer 1994; Tews et al. 2004; Cramer & Willig 2005; Stuessy et al. 2006; Kallimanis et al. 2011; Triantis et al. 2012b). While imprecise definitions and conceptual vagueness may, in some cases, support interdisciplinary, pragmatic and creative scientific activity (Strunz 2012), they also cause misleading data interpretations and conclusions (see Manuscript 5).

The effect of heterogeneity (of different factors) on species diversity is commonly interpreted in the context of niche theory and species coexistence. It is suggested that a larger number of habitats in a specific area or a larger environmental heterogeneity enables a greater number of potential niches, which allow more species to coexist. Following species-specific traits and the resulting resource and environmental requirements, species are sorted spatially in patchy microhabitats (Lundholm 2009; Douda et al. 2012; and references therein). The same sorting

may also take place in time (time patches), a mechanism that is much less understood (see Chapter 1.4.7.). Habitat richness (e.g. Hortal et al. 2009; Panitsa et al. 2010; Manuscript 3) and environmental heterogeneity (Lundholm 2009) have a strong effect on species richness patterns but are less important (if at all) for the distribution of single species (Guisan & Rahbek 2011).

Extensive literature surveys not only show the limited number of studies on the *heterogeneity diversity relationship* but also especially raise the missing theoretical underpinning for negative relationships that have also been reported (Lundholm 2009; Tamme et al. 2010). Douda et al. (2012) suggest that on a local scale, species coexistence may be less affected by environmental niche differentiation than by neutral stochastic processes (Hubbell 2001) or inter- and intraspecific mutualistic interactions (Reynolds et al. 2007; Questad & Foster 2008) as well as non-sexual reproduction and proliferation such as clonal growth (Baer et al. 2004; Reynolds et al. 2007). The fact that species tend to be more aggregated at very small spatial scales than most ecological theories predict supports this suggestion (Manuscript 1).

Dispersal limitations caused by structured landscapes may be another reason why species coexist independent from variability in environmental factors (Garcillán & Ezcurra 2003; Tamme et al. 2010, see Chapter 1.4.2.). In addition, some species are especially adapted to a heterogeneous environment leading to dominance patterns of few species in very heterogenic environments (Lundholm 2009; Tamme et al. 2010).

Heterogeneity measurements differ in the way heterogeneity is quantified and in the focal variable. Heterogeneity, as a correlate for species richness, is for example measured using elevation or geology (Tews et al. 2004; Baldi 2008; Kreft et al. 2008; Kisel et al. 2011; Stegen et al. 2012), by counting different (plant) communities that are arbitrarily defined (e.g. Hortal et al. 2009; Panitsa et al. 2010), by accumulating land cover classes (Kisel et al. 2011), habitat types, vegetation zones, light requirements and water availability (Gehrke & Linder 2011) or via geodiversity (Körner 2007). In his extensive review, Lundholm (2009) identified variability in soil properties or topography as the most common variable to quantify "heterogeneity" (Figure 2 a). Heterogeneity is commonly quantified by a measure of variance or range using single simple coefficients (Figure 2 b,c,d). The few, very recent studies addressing the concept in island biogeography, however, mainly quantified it as the sum of vegetation units (see Manuscript 5). Manuscript 6 highlights the importance to differentiate between aspects of topographic heterogeneity. Six indices are quantified and discussed.

Review studies suspect the significance of a heterogeneity-diversity relationship to be dependent on the scale under study (grain, extent) as well as the part of heterogeneity that is measured (Lundholm 2009; Tamme et al. 2010). Especially very small spatial scales are not studied so far and pose a severe gap in scientific knowledge. Manuscript 6 & 7 thus address micro-heterogeneity on scales smaller 1 m. Both manuscripts could show for two entirely different ecosystems (i.e. medieval castles and Canary Islands pine and laurel forests) that the effect is especially relevant for bryophytes and lichens, but not for herbaceous or woody plant species (Manuscript 6 & 7). This finding was recently confirmed for a temperate swamp forest (Douda et al. 2012). One reason might be that mosses and lichens adhere like a second skin to surfaces while herbaceous plants can escape topographic effects via vertical growth. Douda et al. (2012) suggests that most herbaceous plants are dispersal limited while the distribution of bryophytes is mainly constrained by environmental properties.

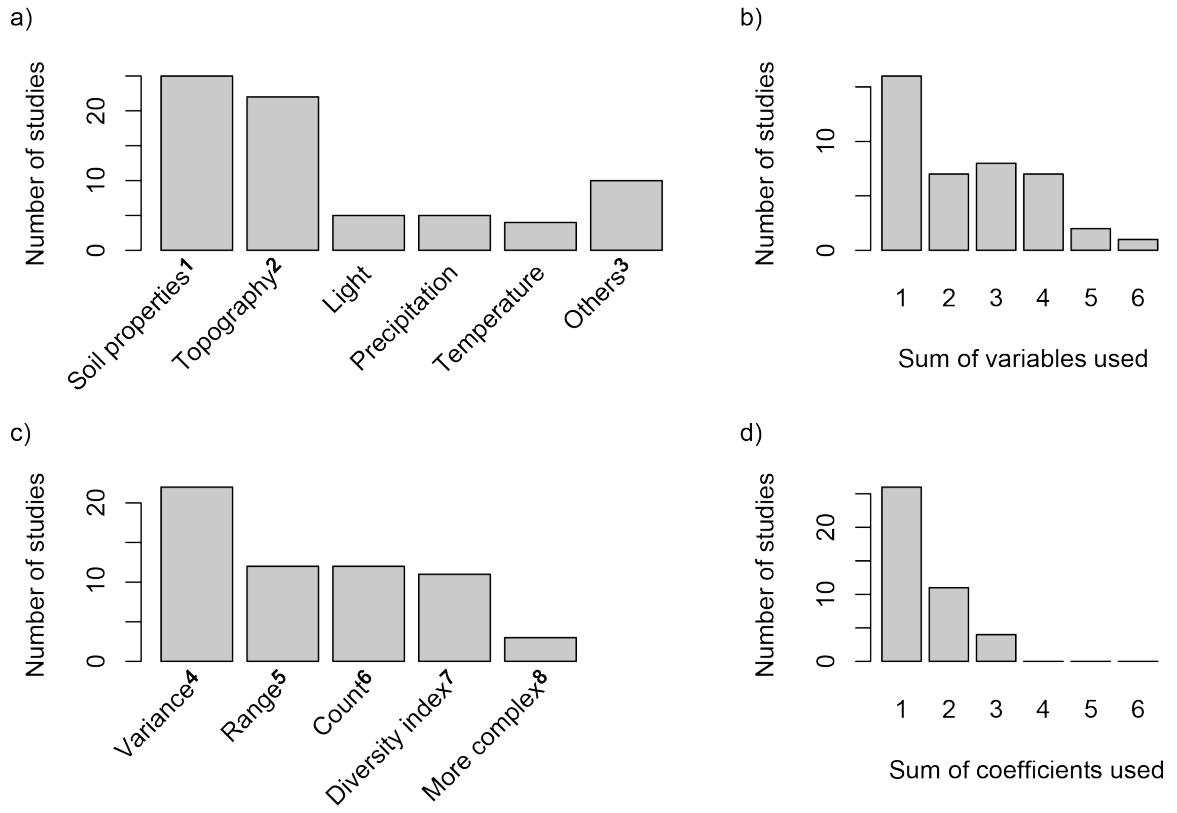

Figure 2: Studies on the heterogeneity-diversity relationship are usually based on soil properties and topography (a & b) and use very simple and a limited number of coefficients (c & d). Manuscript 6 & 7 successfully show that variability in topography can be differentiated into a multitude of aspects that can be quantified. Data extracted from Table 1 in Lundholm (2009). 1) including nutrients, soil type, soil water, soil depth, substrate type, bedrock type and geology; 2) including elevation and topography; 3) including habitat number, vegetation structure or cover, flood frequency, landscape diversity, rock cover, land use, slope and aspect; 4) including standard deviance, coefficient of variance and variance between points; 5) range between minimum and maximum of the variable under focus; 6) the number of different categorically patch types; 7) Shannon-Weiner and Simpsons Index; 8) including nugget variance and fractal dimensions.

"Heterogeneity" as a vague term is part of various ecological theories (e.g. "habitat complexity" in Whittaker et al. 2007). However, it is neither defined precisely nor measured adequately. Thus I claim that before a general validity of the *heterogeneity-diversity relationship* can be assessed, a discussion on proper definitions and measurements of heterogeneity needs to be initiated. The biggest obstacle and largest challenge regarding *heterogeneity-diversity relationship* is its imprecise terminology and the unclear measurement of "*heterogeneity*". One possibility for the confusion is the difference in the understanding of "habitat". While it is partly used species-specific indicating the living conditions of a specific species (e.g. Tscharntke et al. 2012), a habitat seems especially among native Anglophones to be understood as a vegetation unit. Even in the famous *habitat heterogeneity hypothesis* "*heterogeneity*" is defined as the sum of habitats (Cramer & Willig 2005) as well as "*heterogeneous environment*" (Douda et al. 2012). Already Nilsson et al. (1988) (and again Gehrke & Linder 2011 and Manuscript 5) criticised the imprecise terminology and highlighted differences between for instance *habitat heterogeneity* and *habitat diversity*.

Diversity at the level of habitats includes qualitative (i.e. contrast and similarity), quantitative (i.e. number of types and units) and functional aspects (i.e. diversity of processes leading to

high or low complexity). Thus, heterogeneity as a spatial arrangement should not be directly confounded with complexity, which is a process-oriented functional term, even if heterogeneity and complexity are likely to be correlated. Furthermore, qualitative, quantitative and functional aspects between-habitats and within-habitats have to be differentiated. An entirely different terminology is used when heterogeneity is quantified in a temporal context (e.g. Buhk et al. 2007).

The unclear and inconsistent use of terms does not only hinder a proper integrative conclusion on the heterogeneity-diversity relationship but favours misinterpretation of sound scientific findings. The ultimate cause for Manuscript 5 was a misunderstanding by Kallimanis et al. (2011), who interpreted an islands elevation as a proxy for habitat heterogeneity that is said to stimulate speciation. This reasoning is unexpectedly frequent (e.g. Gehrke & Linder (2011). In fact *habitat heterogeneity* is used for a number of different phenomena. Topographic heterogeneity or the number of habitats is among those drivers, which are not proven to increase speciation rate *per species* in general. Manuscript 5 provides a detailed discussion which aspects or concepts of habitat heterogeneity might promote speciation and why this effect needs to be differentiated from an effect of elevation. The results of Kallimanis et al. (2011) are reinterpreted in this context.

1.4.7. Diversity-time relation

Temporal aspects and their effects on diversity via colonisation, extinction and speciation are much less investigated and understood than spatial drivers. However, spatial patterns at any given time likely originate from dynamic processes. Their causes may only be understood over longer periods where they affect species development, coexistence and extinctions (Preston 1960; White et al. 2010). The highly dynamic taxon cycle of alternating colonisation and speciation periods (Wilson 1959, 1961) for instance appears to be static at scales of human perception (Ricklefs 2012). The importance of time is also increasingly recognised for instance in current island biogeographical theory (Whittaker et al. 2007, 2008, 2010; Fernández-Palacios et al. 2011).

"Time" influences diversity via multiple mechanisms. Environmental fluctuations on ecological time scales affect species diversity (e.g. *intermediate disturbance hypothesis*, see Svensson et al. 2012) and are highly relevant for multiple ecosystem properties and the distribution of species (Jentsch et al. 2011). Individual biota are often adapted to the present disturbance regime or may even "*learn*" from extreme events within their life span ("stress memory"; Kreyling et al. 2012a, Kreyling et al. 2012b, Walter et al. 2012). Rare environmental situations may also initiate shifts in ecosystems (Kreyling et al. 2011). In addition, time needs to pass for processes to cause a pattern (e.g. species accumulation; Stephens & Wiens 2003). Finally case specific history, i.e. time lags between causal driver and resulting patterns (e.g. influence of paleoclimate, persistence, land use history etc.; e.g. Aggemyr & Cousins 2012; Kissling et al. 2012) influences current biotic patterns.

Scientists are also increasingly focussing on the relation between temporal species turnover and other influential factors like regional diversity, productivity and habitat heterogeneity (Stegen et al. 2012). It is e.g. suggested that less species rich regions tend to face a fast temporal species turnover due to more stochastic processes involved in defining species occurrence patterns (Stegen et al. 2012). The temporal turnover of species results in an increase in dissimilarity of species assemblages between time steps (time-decay; Korhonen et al., 2010; Chapter 1.4.2.). The term *species-time relationship* was originally associated to sampling i.e. an increase in species richness with sampling time (Rosenzweig 1995). However, it has meanwhile been recognised that temporal species turnover is quite effective on ecological and paleoecological timescales (White et al. 2010 and references therein) and that it increases with spatial environmental heterogeneity (White et al. 2010). It is widely recognised that past disturbance regimes (e.g.

land use) may contribute to species richness patterns in an equal manner than current conditions (Aggemyr & Cousins 2012). The detection of historic influences is often hindered by a strong correlation of current and historic conditions (Hortal et al. 2011). Species succession after major disturbances on novel substrate or island formations takes time (Whittaker et al. 1989) and species composition changes with time even without an alteration of the external environmental settings (Adler et al. 2005). Despite claims that speciation and colonisation processes can be effective at similar time-scales (Carroll et al. 2007), the initial colonisation of novel habitats is, even on newly emerging oceanic islands, relatively fast in comparison to speciation processes (Whittaker et al. 1989).

The importance of the *time for speciation effect* (Stephens & Wiens 2003) for diversity pattern is increasingly recognised, but its relative importance is under debate (McPeek & Brown 2007; Ricklefs 2007; Linder 2008; Rabosky 2009). Despite the evidence that niche conservatism and time for speciation are responsible for a multitude of diversity patterns, it is remarkably seldom tested or considered (Wiens et al. 2010). Especially the diversity of most lineages increases with time, a fact that has been proven for African sky mountains (i.e. island like mountains see Chapter 1.4.5. & 1.5.), where older lineages also host most species and areas first reached by certain lineages host the highest diversity (Gehrke & Linder 2011).

Many of the patterns, phenomena and traits we find today have ancient roots that cannot be understood only based on present day conditions (Wiens et al. 2010; Kissling et al. 2012). It has e.g. been shown that the current species richness patterns are not only defined by current climatic conditions and barriers, but also to a high degree by the colonisation pathways from climatic refugia, where species e.g. managed to survive the last ice age cold cycles (Svenning & Skov 2007; Essl et al. 2011; Hortal et al. 2011; Allcock & Strugnell 2012). Thus Quaternary climate fluctuations and pre-Quaternary climate conditions have their legacy in current species distribution patterns (Kissling et al. 2012). Especially the diversity pattern in mid to high latitude landscapes is strongly affected by postglacial dispersal limitations. A delayed Holocene recolonisation still influences the distribution of many alpine plants (Dullinger et al. 2012). Thus information on historic climate and species distribution is crucial in order to understand the development of species distribution over time (Fraser et al. 2012; Maiorano et al. 2012).

For oceanic islands a specific ontogeny of island development with time has been illustrated (Whittaker et al. 2007; Fernández-Palacios et al. 2011). The interaction of volcanic and geomorphological processes provides a typical set of environmental circumstances depending on the age of an island, also resulting in a specific pattern of diversity (Whittaker et al. 2008, 2010). The currently most comprehensive theory is the *general dynamic model of island biogeography* (GDM, Whittaker et al. 2008). The GDM especially emphasises the importance of island age for the diversity on a focal island and integrates the processes of colonisation, speciation and extinction in one comprehensive theory in line with the characteristic ontogeny of a volcanic oceanic island. After a volcanic emergence over sea surface, islands are in general transformed by erosion processes making the island first more heterogeneous and then finally flatter (Whittaker et al. 2007). In addition, for some island systems, the elevation is gradually reduced by subsidence of the underlying tectonic plate, once the volcanic hotspot responsible for its existence has passed by (Fernández-Palacios et al. 2011). Whittaker et al. (2008) suggest that the carrying capacity of an island, which they related to habitat heterogeneity (see Chapter 1.4.6.), will increase with an island growing in area and elevation and decline when an island is heading towards submergence. They also conclude that speciation is strongly dependent on the age of a specific island with age integrating several island characteristics including the time available for speciation itself. With that Whittaker et al. (2008) contradict Emerson & Kolm (2005) who predicted an increasing diversification with species richness proving it with data form the Hawaiian Islands and the Canary Islands. This *diversity begets diversification* hypothesis has induced a controversial discussion (Cadena et al. 2005; Kiflawi et al. 2007; Pereira et al. 2007; Whittaker et al. 2007, Witt & Maliakal-Witt 2007; Birand & Howard 2008; Gruner et al. 2008; Vilenkin et al. 2009; Manuscript 2).

Both, Emerson & Kolm (2005) and Whittaker et al. (2008) use the percentage of single island endemic species (pSIE) as an indicator for diversification and prove their hypothesis by a positive relation of pSIE with species richness (Emerson & Kolm 2005) or a hump shaped relation with age (Whittaker et al. 2007, 2008). The latter finding however was based on flawed statistics (Manuscript 4), but nevertheless holds a re-evaluation with adequate statistical analyses (Bunnefeld & Phillimore 2012, Manuscript 4).

Ice age extinctions (Svenning & Skov 2007) but also island biogeography (Fernández-Palacios et al. 2011) stress the importance of stable environmental conditions for species richness over long time spans. On many archipelagos species are "transferred" from older vanishing islands to newly ones evolved (Fernández-Palacios et al. 2011). Thus, while the geomorphological system of an archipelago is highly dynamic on geological time scales, hot spot archipelagos deliver relatively constant environmental conditions for biota if they manage to move from old to newly emerging islands. The long-term survival chance of biota on an oceanic island is thus dependent on the reoccurring presence of new islands, which is in turn dependent on the geophysical characteristics of the underlying tectonic anomaly. I thus hypothesise that those geophysical characteristics might in parts be suitable to predict species richness on entire archipelagos, once effects of isolation and climate have been controlled for.

1.5. Island biogeography and a change in diversification along elevational gradients

1.5.1. Elevation induces ecological isolation

Almost 50 years ago MacArthur & Wilson (1963) provided a concept linking ecological processes with observable species diversity patterns in their *equilibrium theory on island biogeography*. The idea of a constant species richness that is defined by island specific geographical properties (but with changing species composition) was ground-breaking and has influenced research and discussion in all fields of ecology (Vitousek 2002; Whittaker & Fernández-Palacios 2007). Still, island biogeography is stimulating the development of ecological theory in general. With an increasing understanding of island-like biological systems, strong calls for an incorporation of further aspects (especially temporal and evolutionary dynamics) into a general theory have been addressed (e.g. Brown & Lomolino 2000; Heaney 2000; Lomolino 2000a; Whittaker 2000; Heaney 2007). Meanwhile strong contributions (Whittaker et al. 2007, 2008; Rosindell & Phillimore 2011 with remarks in Manuscript 4) head towards a new synthesis for a general theory of island biogeography. Additional theoretical contribution to island biogeography will probably be enhanced by the public awareness of the 50 years anniversary of the MacArthur & Wilson (1963) paper in 2013.

The hump shaped relation between the percentage of endemic species (pSIE) with island age and a positive relation with species richness has initiated an intense debate on the drivers of evolutionary processes on oceanic islands (Chapter 1.4.7.). While investigating the geo-ecological factors driving species diversity on the Canary Islands (Manuscript 2) I could identify first hints that other factors than a direct effect of age or species richness is responsible for the observed relations of pSIE with age and species richness. Overall species richness is on oceanic islands in general, but on the Canary Islands in particular, positively related to an island´s maximum elevation (Manuscript 2). However, the differentiation between the effect of elevation and age is limited by the strong negative relation between the two variables within the characteristic ontogeny of volcanic islands.

I suggest that the positive relation between pSIE and elevation identified when using entire islands as units comes from an increasing pSIE with elevation within these islands. The underling ecological explanation is an increasing ecological isolation with elevation on islands leading to a higher isolation and thus speciation in higher elevated parts of an island in comparison to the low elevation ecosystems (Figure 1 in Manuscript 2 and Figure 1 in Manuscript 5). On the Canary Islands the closest comparable elevations to the Pico de Teide (3718 m, Tenerife)

occur in the High Atlas Mountains of Morocco (Djebel Toubkal, 4167 m) at a distance of ca. 900 km. This distance is by far larger than the direct distance from coast to coast (ca. 100 km). Thus diaspores or potential colonising individuals from ecosystems with similar environmental conditions have a much stronger dispersal filter for high-elevation ecosystems in comparison to low elevation ecosystem (Manuscript 2 & 5). This directional ecological filtering along the elevational gradient is crucial for the colonisation of non-native species into high-elevation regions worldwide (Alexander et al. 2011) and leads to an increasing isolation with elevation. Species exchange among elevational bands is limited due to niche conservatism and the associated climatic barriers (see Wiens et al. 2007 for further references). The result of this *elevation-driven ecological isolation* hypothesis (Manuscript 2 & 5) is an increasing speciation with elevation resulting in a higher pSIE in higher elevated insular ecosystems. The hypothesis is supported by data from Mediterranean islands (Manuscript 5) as well as the Canary Island (Manuscript 2) and the application of mixed effects models to account for differences among islands (Hortal 2012). Whittaker et al. (2008) interpreted the influence of age primarily via its effect on topographic complexity and carrying capacity on islands. Interestingly, not only an increase of pSIE with elevation but also the hump shaped relation with age within similar elevational bands on different islands was confirmed. This stresses time as an independent driver for evolutionary dynamics.

There are only very few general patterns in ecology. However, there are first hints that the elevation-diversification pattern identified within this thesis may be one of them (Manuscript 2 & 5; Jump et al. 2012). Even within mountain chains such as the European Alps, dispersal limitation (or recolonisation limitation) is a likely cause of the high rate of endemic species around areas suspected to be climatic refugia during the ice age (Dullinger et al. 2012). It has indeed been shown that species distribution of endemic species is strongly influenced by limited post-glacial migration (Essl et al. 2011). Thus environmental filtering along elevational gradients (Alexander et al. 2011) together with the isolating effect induced by dispersal limitation of species and the geographical isolation in high-elevation ecosystems may cause similar changes in speciation with elevation on most mountain systems that are old and large enough to document this process. Especially "sky islands" - i.e. mountains that differ remarkably in their environmental setting from the surrounding matrix - pose optimal study objects but are surprisingly seldom studied (Gehrke & Linder 2011; Nogué et al. 2012). Körner (2007) introduced the idea of an "archipelago of climatic mountain islands" to highlight the distinct *elevation-driven ecological isolation* (Manuscript 2 & 5). As there is a general lack of studies investigating changes in speciation, extinction and colonisation along elevational gradients (Wiens et al. 2007) future studies addressing these issues (see Chapter 1.7.) may not only pose valuable results, but especially contribute to the theoretical understanding of biotic systems.

1.5.2. The effect of isolation on the speciation-elevation interaction

The *elevation-driven ecological isolation* hypothesis (Manuscript 2) indicates above average speciation in high elevations (Manuscript 2 & 5). This is exactly what is found on the Canary Islands (Manuscript 2) and in the Mediterranean (Manuscript 5). On the contrary, knowledge gained from investigations of the latitudinal diversity gradient (Chapter 1.4.4.) and species-area relations (Chapter 1.4.3.) suggests the opposite, namely enhanced speciation in low elevations (Figure 3). First, the *metabolic theory of ecology* strongly favours an increase of speciation rate with temperature or more general with available energy. The above average speciation rate in warm areas originates either form a direct effect via fast rates of speciation or due to a larger number of individuals in comparison to cold areas (Rohde 1992). Second, the larger number of species found in low to mid elevations (Alexander et al. 2011) is claimed to enhance speciation via interspecific interactions and pressure for adaptive radiation (*diversity begets diversity*; Emerson & Kolm 2005). Third, no matter whether speciation *per species* increases with area linearly or via thresholds (Lomolino 2000b; Losos & Schluter 2000; Kisel & Barraclough 2010)

it would be above average in low elevations where the area of altitudinal belts tends to be larger (Körner 2007). Forth, extinction rates are suspected to be higher in temperate than in tropical climates (Weir & Schluter 2007), which could be reflected in an increase in extinction rate with elevations (McCain 2009). MacArthur (1972) already denoted enhanced extinction rates in mountain environments due to the small area and high isolation. High extinction risk of species results in a fast temporal species turnover. The resulting low time available for each species likely additionally decreases the chance of one species for adaptive radiation (*time for speciation* hypothesis; Stephens & Wiens 2003).

Time for speciation has been suggested as a causal explanation for richness patterns along elevational gradients with clades in low to mid elevations being older then in high elevation (Wiens et al. 2007). Wiens et al. (2007) suspects an above average diversification rate at mid elevations and highlight that it may be caused either by an increased speciation rate at mid elevations or by a increased extinction rate at high and low elevations. However, Wiens et al. (2007) do not consider any elevational movement of species, a fact that may indeed become more and more relevant in face of climatic changes (Jentsch & Beierkuhnlein 2003). Species diversity and hence intensified species interactions have in addition been suggested to enhance extinction risk of single species (*diversity begets diversity*; Emerson & Kolm 2005). In summary, taking away the effect of isolation, which is one prerequisite for speciation (Heaney 2000), theory predicts a higher rate of speciation and especially diversification in low, not in high elevations (Figure 3).

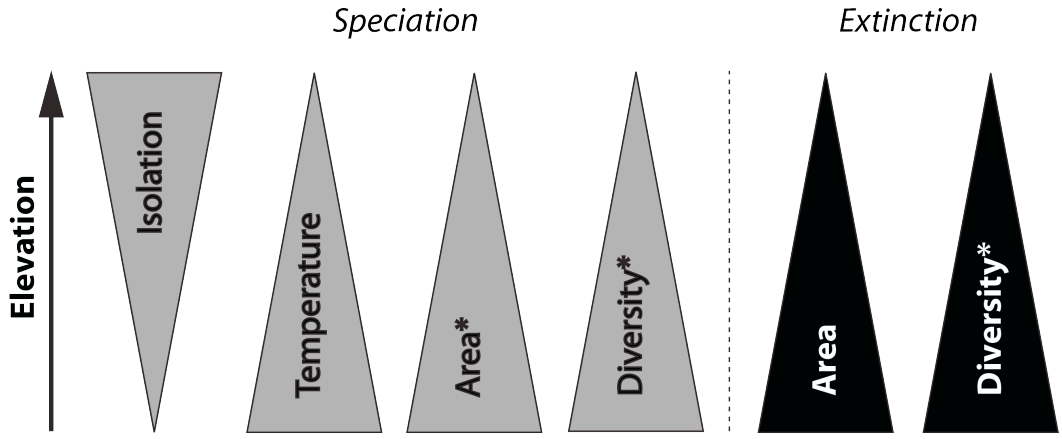

Figure 3: The elevational dependence of different drivers of speciation (grey) and extinction (black) on diversification of species along an elevational gradient of a high oceanic island. Only elevation-driven ecological ***isolation*** *supports higher speciation and thus diversification rates in high-elevation ecosystems on islands (and mountains). The opposite effect is triggered by* ***temperature****,* ***area*** *and* ***diversity dependent interactions*** *among a smaller number of species. *)Asterisks indicate mechanisms that are under debate.*

The effect of elevation-driven ecological isolation diminishes if the difference in isolation between high and low elevation ecosystems declines. On very remote oceanic islands like Hawaii high and low elevation ecosystems are both equally isolated from a continental source region, while on Crete, high and low elevation ecosystems differ considerable in distance to comparable ecosystems on the mainland (Figure 1 in Manuscript 5). As a consequence, I expect a counterintuitive interaction between the relation of diversification with elevation and the degree of isolation of islands. For continental mountains the isolation contrast between low and high elevations is very strong as low elevations directly merge into the surrounding matrix. Here and for less isolated islands, I expect a significant increase in diversification processes with elevation. This would be reflected by an above average pSIE in high elevations if the

mountains are large enough to support speciation and old enough to document the pattern. I expect that the more isolated an island is, the less pronounced is the positive relation of diversification (and pSIE) with elevation. Ultimately, if the contrast in isolation becomes negligible, the diversification-elevation relation should be reversed with higher or at least equal diversification rates in low elevation (Figure 4). The theory – yet to be tested – does however not question the comparably high rates of diversification (and thus endemism) on isolated islands.

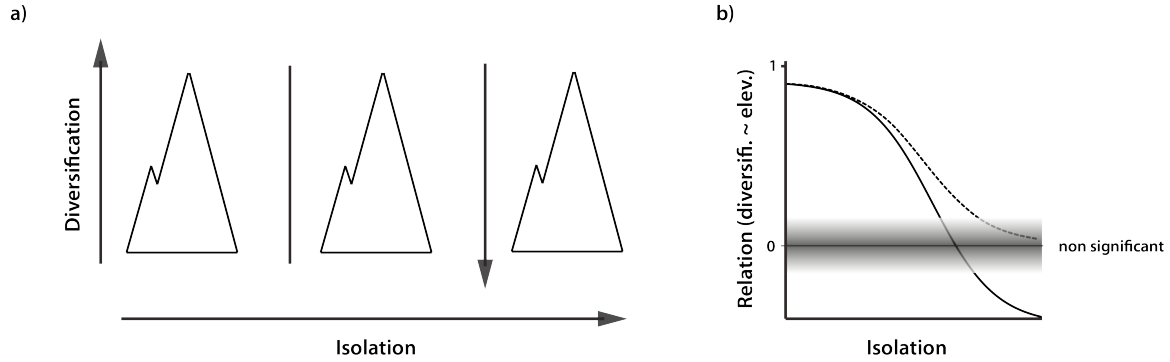

Figure 4: The increase in diversification with elevation should be reduced with increasing isolation of the island (a & b). The more isolated an island is the less pronounced is the difference in isolation of its low and high elevation ecosystems. Whether diversification per species on very remote islands more prominent in low elevation ecosystems, as predicted by theory (continuous line), or not (dashed line) is yet to be tested.

1.6. Manuscripts of this thesis

Scientific disciplines "*typically cycle between periods of empiricism and theory, reductionism and holism*" (West & Brown 2005). Usually involved individuals specialise in one of both approaches. This thesis contains both, empirical as well as theoretical manuscripts and covers a broad range of approaches and study regions. As there is a general lack of considering and questioning underling assumptions when testing ecological theory (Austin 2007) I provided a general overview on the current theoretical framework within the introduction. In the following I briefly show how the manuscripts of this thesis - all dealing with plant species richness and composition - relate to the current state of knowledge of diversity patterns and their drivers.

Manuscript 1 provides a comprehensive review on distance-decay analyses, the most prominent pattern of species assemblages. It is shown that the scale dependent differences in the measured spatial turnover of species are not necessarily the result of ecological drivers operation on different scales. By using simulated landscapes and sampling schemes, it questions the currently used methodology. The general assumption that the methodology is independent from grain size and study extent is not valid. Novel tools for analyses of spatial decay of community composition similarity need to be developed.

Strong turnover in species composition is not only observable in horizontal space, but is particular observable along elevational gradients as a result of environmental filtering. **Manuscript 2** demonstrates that this results in an increase of isolation of higher elevated ecosystems, as regions with comparable environmental conditions are both, farer apart and smaller in area. The resulting decline in species colonisation should decrease genetic exchange and increases speciation rate per species. Using elevation specific data from the Canary Islands it is shown that the percentage of endemic species (pSIE) increases with elevation. This fact is interpreted as an increase in diversification with elevation. The results show that the increase of pSIE with

species richness that was claimed to be a proof for the *diversity begets diversification hypothesis* (see Chapter 1.3.4.) may be an artefact of island elevation.

Manuscript 3 performs an in-depth analysis of environmental and anthropogenic correlates for species richness, endemism and turnover in species composition on the Canary Islands. Here I identify the importance of island elevation not only on species richness but also on the degree of endemism leading to the subsequent conceptual idea for the *elevation-driven ecological isolation hypothesis* further elaborated and tested in Manuscript 2. **Manuscript 3** also compares distance-decay of various species groups and identifies environmental correlates and discusses possible causalities for the pattern in species richness and composition in the context of current island biogeographical theory.

Manuscript 4 corrects a statistical mistake in one of the most important manuscripts on island biogeography. The previously applied regression analyses are repeated applying an adequate significance test. In addition, mixed effect models are used to show if the theoretical predictions are generally confirmed by data. It is also shown that area is more important for species richness than for endemic richness or the percentage of endemic species (both indication evolutionary dynamics). A further important result is that in a typical ontogeny of volcanic islands species richness reaches its maximum before the number and degree of endemism is peaking.

Manuscript 5 further deepens the idea of the *elevation-driven ecological isolation* (Manuscript 2 & 3). It is shown that the observed pattern of an increase of the degree of endemism with elevation is especially observable on old continental islands (here Crete and Corsica). This was important as other authors claimed elevation being a proxy for habitat heterogeneity to be responsible for the pattern. It is clarified that environmental heterogeneity may enhance speciation per species, but that the mechanism is different from the *elevation-driven ecological isolation* and needs jet to be tested.

Heterogeneity and its effect on plant species composition and richness is the core focus of **Manuscript 6 & 7**. **Manuscript 6** introduces indices to quantify different aspects of wall surface heterogeneity using Franconian castle walls as a case study. It is demonstrated that different aspects of surface morphology (i.e. gap frequency, size, amplitude etc.) affect richness and composition of wall vegetation. Especially lichens are sensitive to surface properties. The results are used to initiate a discussion on environmental friendly restoration of historic buildings. **Manuscript 7** relates micro-topography to species richness in habitats along an elevational gradient on La Palma, Canary Islands. Here, the occurrence of bryophytes is strongly dependent on wall surface heterogeneity, while herbs and woody plants again show little response to alteration in micro-topography (at least on the studies scale).

Manuscript 8 assesses effects of human impact on patterns of species richness and composition. Enclosures established over a decade ago for nature conservation purpose are used to show the dramatic degrading effect that introduced herbivores have on high-elevation ecosystems on La Palma, Canary Islands. The ecosystem is nearly entirely structured by leguminous endemic shrub species. Manuscript 8 elaborates indications for a regime shift in species composition from a species rich to a mono-dominant species assembly. The regime shift was likely caused by grazing goats and is now adhered by introduced rabbits.

1.7. Outlook

1.7.1. Scientific development

While my first manuscript (Manuscript 3) concentrates on the detection of diversity patterns, the following work tackles existing theoretical knowledge (e.g. Manuscript 2 & 5) or methodological approaches (e.g. Manuscript 1 & 4). Ricklefs (2012) recently claimed, "*observation often is used to serve theory rather than to test predictions and find inspiration for new ideas*". Fieldwork and biodiversity assessments, however, must not stay at a descriptive and mere observational level. In fact, previously accepted and prominent hypotheses have been questioned in the frame of this thesis (Chapter 1.3.4., 1.4.6. & 1.5.1.). Several important questions and further research challenges have been identified or directly arise from the findings of this thesis.

1.7.2. Island Biogeography

A novel hypothesis elaborated in this thesis is the interaction between island isolation and the elevation-diversification relationship (Chapter 1.5.2.). The question is, whether the increase in the percentage of endemic species with elevation observed on Mediterranean islands and the Canary archipelago (Manuscript 2 & 4) is a global phenomenon or if it becomes reversed on very isolated islands as predicted by my theoretical considerations (Chapter 1.5.2.). This hypothesis will be tested in a next step with a global dataset. The focus on elevational gradients is especially promising as montane ecosystems are hotspots of biological diversity (Lomolino 2001) and very relevant for conservation (Wiens et al. 2007). Pooling data of different origin, however, needs a careful evaluation of quality and comparability and rigorous statistical testing of the hypothesised pattern (Lomolino 2001).

A positive relation between speciation rate *per species* with area has been postulated and tested by a number of studies on island systems (Lomolino 2000b; Losos & Schluter 2000; Stuessy et al. 2006; Kisel & Barraclough 2010). While the idea of a positive speciation-area relationship becomes commonly accepted (e.g. Givnish 2010), none of the mentioned studies was able to clearly differentiate effects of area from effects of elevation (via elevation-driven ecological isolation, Manuscript 2 & 5). In addition, a relation of speciation with habitat heterogeneity ("*topographic diversity*" in Losos & Schluter 2000) is acknowledged (Chapter 1.3.4.). Losos & Schluter (2000) stress that they cannot exclude an influence of elevation on speciation as all islands with a high number of speciation events are high in elevation. A differentiated investigation that is explicitely addressing the prediction of a positive speciation-area relationship would help to disentangle the drivers of speciation *per species*. This approach could adopt methodologies developed in Manuscript 6 & 7 and apply them to a similar set of islands used by Kisel & Barraclough (2010).

1.7.3. Ecological saturation

Rosenzweig (1995) highlighted the fascinating connection between speciation and overall species richness. He suggests, "*competitive speciation is fuelled by ecological opportunity*". Speciation should thus decline with an increase in the number of species. However, in another part of his book Rosenzweig (1995) acknowledges, "*species can be niches for other species*". As discussed (Box 1) this antagonism of the implicit acceptance of a carrying capacity of ecological systems in theoretical considerations and a simultaneous knowledge of open communities and differences in species richness among sites of comparable environmental properties is quite common among ecologists (Ricklefs 2006a). Givnish (2010) highlights this issue as one of the remaining fundamental questions. "*What is the evidence of ecological saturation? Over what timescales does such saturation occur, and in what circumstances?*" (Givnish 2010). Research on saturation however, is a non-trivial task. The main challenge

besides quantifying all relevant environmental and biotic drivers is the investigation of different temporal scales.

1.7.4. Integrating space and time

Studies on species diversity that integrate both, space and time, in a way that their explanatory contribution can be identified are rare (White et al. 2010; Stegen et al. 2012). Today, the increased exchange and availability of data offers new opportunities to partly fill this research gap. Temporal aspects, however, are not just another variable that can be integrated along with area and distance. Moreover in the same way as sampling effort increases when changing from linear to a two-dimensional area-wide sampling approach, the complexity changes when adding time as another dimension. Depending on the system under focus the time lag between historic influences and current patterns may span palaeontological scales (Beck et al. 2012), or involve short-term fluctuations, where a very high temporal measurement resolution is needed. The challenge is to identify only the relevant drivers that may be temporarily reoccurring, event like or gradual.

Interestingly, current considerations in other fields such as community-ecology borrow ideas from island biogeography (White et al. 2010). Seemingly, the spatial and temporal distinctness of island systems enables the identification and quantification of relevant processes and drivers. The typical ontogeny of oceanic islands and their spatial arrangement makes them especially useful when investigating diversity patterns and their drivers. There is increasing evidence that oceanic island archipelagos need to be studied as combined systems rather than each island separately. Biota move from older to younger islands. Lineages may have been on the archipelago and its precursors longer than the age of the oldest current island due to the fact that archipelagos exhibit also a history of past islands (Fernández-Palacios et al. 2011). Geophysical properties of the melting anomaly that are responsible for the constant development of new volcanic islands may influence the temporal performance of islands in geological time scales and thus the overall species richness of the archipelago. While the overall number of oceanic island archipelagos is limited, they are relatively well studied, which makes a further investigation and test of this hypothesis not only worthwhile but also feasible.

1.7.5. Heterogeneity

The use of "habitat heterogeneity" in ecological studies is far from being unanimous. Imprecise wording and understanding of terms such as *habitat heterogeneity*, *habitat diversity*, *environmental complexity* especially in theoretical considerations is hindering rigours hypothesis testing (Chapter 1.4.6.). It can even lead to wrong conclusions (Manuscript 5). I have shown that an efficient quantification of the different aspects of *heterogeneity* is possible (Manuscript 6 & 7). What is missing is a comprehensive work that reviews the existing usage and implicit or explicit definitions of the *heterogeneity*-associated wording. Providing precise frameworks and concepts will illuminate a path through the jungle of *heterogeneity* in order to integrate its important aspects adequately in current theoretical considerations.

1.8. List of manuscripts and declaration of own contribution

Manuscript 1:
Authors: Steinbauer, M; Dolos, K; Reineking, B; Beierkuhnlein, C
Title: **Current measures for distance decay in similarity of species composition are influenced by study extent and grain size**
Journal and status: ***Global Ecology and Biogeography***, 21, 1203–1212 (2012)
Own contribution: data analysis and figures: 50%, writing: 85%; concept and discussion: 80%; corresponding author

Manuscript 2:
Authors: Steinbauer, M; Otto, Rüdiger; Naranjo-Cigala, A; Beierkuhnlein, C; Fernández-Palacios, JM
Title: **Increase of island endemism with altitude – speciation processes on oceanic islands**
Journal and status: ***Ecography***, 35, 23-32 (2012)
Own contribution: data acquisition: 0%, data analysis and figures: 100%, writing: 90%; concept and discussion: 90%; corresponding author

Manuscript 3:
Authors: Steinbauer, M; Beierkuhnlein, C
Title: **Characteristic pattern of species diversity on the Canary Islands**
Journal and status: ***Erdkunde***, 64, 57-71 (2010)
Own contribution: data acquisition: 100%, data analysis and figures: 90%, writing: 90%; concept and discussion: 80%; corresponding author

Manuscript 4:
Authors: Steinbauer, M; Dolos, K; Reineking, B; Beierkuhnlein, C
Title: **Revaluating the general dynamic theory of oceanic island biogeography**
Journal and status: ***Frontiers of Biogeography***, submitted
Own contribution: data analysis and figures: 70%, writing: 85%; concept and discussion: 85%; concept and discussion: 90%; corresponding author

Manuscript 5:
Authors: Steinbauer, M; Irl, S; Beierkuhnlein, C
Title: **Elevation-driven ecological isolation promotes diversification on Mediterranean islands**
Journal and status: ***Acta Oecologica***, 47, 52-56 (2013)
Own contribution: figure: 25%, writing: 75%; concept and discussion: 75%; corresponding author

Manuscript 6:
Authors: Steinbauer, M; Gohlke, A; Mahler, C; Schmiedinger, A; Beierkuhnlein, C
Title: **Quantification of wall surface heterogeneity and its influence on species diversity at medieval castles - implications for the environmentally friendly preservation of cultural heritage**
Journal and status: ***Journal of Cultural Heritage***, 14, 219-228 (2013)
Own contribution: field work: 0%, data analysis and figures: 60%, writing: 75%; concept and discussion: 50%; corresponding author

Manuscript 7:
Authors: Leutner, B; Steinbauer, M; Müller, CM; Früh, AJ; Irl, S; Jentsch, A; Beierkuhnlein, C
Title: **Mosses like it rough - Growth form specific responses of mosses, herbaceous and woody plants to micro-relief heterogeneity**
Journal and status: ***Diversity***, 4, 59-73 (2012)

Own contribution: field work: 0%, data analysis and figures: 5%, writing: 20%; concept and discussion: 30%; corresponding author

Manuscript 8:
Authors: Irl, S; Steinbauer, M; Babel, W; Beierkuhnlein, C; Blume-Werry, G; Messinger, J; Palomares-Martínez, A; Strohmeier, S; Jentsch, A
Title: **An eleven-year exclosure experiment in a high-elevation island ecosystem: Introduced herbivore impact on shrub species richness, seedling recruitment and population dynamics**
Journal and status: ***Journal of Vegetation Science***, 23, 1114-1125 (2012)
Own contribution: field work: 20%, data analysis and figures: 75%, writing: 20%; concept and discussion: 20%

1.9. Acknowledgements

I had a great time while working on the manuscripts that culminate in this thesis. I owe my thanks to a large number of people and want to particularly mention some of them.

I especially would like to thank Carl for guidance, confidence, financial independency, freedom of research and for inspiration. My life, my motivation and thinking have changed in the past years and it is you that made this possible!

I am also very grateful of Anke for a lot but especially for her support in a critical situation.

David and Severin are great! There is nothing more to say.

Jürgen and Reinhold were always the first, last and most reliable if help was needed.

I thank Klara and Björn for all I know about statistics and a lot more!

And Martin for being who he is.

I have to express my graditude to a number of excellent anonymous reviewers and journal editors, among them especially Joaquín and José María. You did a great job in teaching me how to communicate science.

Kai was very influencial during a critical period in winning my heart for ecology.

I thank Heidi and Volker for being the mum and dad I would have chosen.

My kids Aaron, Aeneas and Ronja were neither patient nor supportive of this thesis. Despite that I owe them for bringing a lot more richness and meaning to my life.

Above all, I thank Michaela for being such a wonderful person.

1.10. References of Introduction

Adler PB, White EP, Lauenroth WK, Kaufman DM, Rassweiler A, Rusak JA (2005) Evidence for a general species–time–area relationship. *Ecology* **86**, 2032–2039.

Aggemyr E, Cousins SAO (2012) Landscape structure and land use history influence changes in island plant composition after 100 years. *Journal of Biogeography* **39**, 1645-1656.

Alexander JM, Kueffer C, Daehler CC, Edwards PJ, Pauchard A, Seipel A, MIREN Consortium (2011) Assembly of nonnative floras along elevational gradients explained by directional ecological filtering. *Proceedings of the National Academy of Sciences* **2**, 656-661.

Allcock AL, Strugnell JM (2012) Southern Ocean diversity: new paradigms from molecular ecology. *Trends in Ecology and Evolution* **27**, 520-528.

Allen AP, Gillooly JF (2006) Assessing latitudinal gradients in speciation rates and biodiversity at the global scale. *Ecology Letters* **9**, 947–954.

Almeida-Neto M, Guimarães P, Guimarães PR, Loyola RD, Ulrich W (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* **117**, 1227-1239.

Anthelme F, Dangles F (2012) Plant–plant interactions in tropical alpine environments, Perspectives in Plant Ecology. *Evolution and Systematics* **14**, 363-372.

Arrhenius O (1920) Distribution of the species over the area. *Meddelanden från K. Vetenskapsakademiens Nobelinstitut* **4**, 1–6.

Arrhenius O (1921) Species and area. *Journal of Ecology* **9**, 95–99.

Austin MP (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling* **157**, 101-118.

Austin MP (2007) Species distribution models and ecological theory: A critical assessment and some possible new approaches. *Ecological Modelling* **200**, 1-19.

Baer SG, Blair JM, Collins SL, Knapp AK (2004) Plant community responses to resource availability and heterogeneity during restoration. *Oecologia* **139**, 617-629.

Baldi A (2008) Habitat heterogeneity overrides the species-area relationship. *Journal of Biogeography* **35**, 675–681.

Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* **19**, 134–143.

Beck J, Brehm G, Fiedler K (2011) Links between the environment, abundance and diversity of Andean moths. *Biotropica* **43**, 208-214.

Beck J, Ballesteros-Mejia L, Buchmann CM, Dengler J, Fritz SA, Gruber B, Hof C, Jansen F, Knapp S, Kreft H, Schneider A-K, Winter M, Dormann CF (2012) What's on the horizon of macroecology? *Ecography* **35**, 1-11.

Beierkuhnlein C (1998) Biodiversität und Raum. *Die Erde* **128**, 81–101.

Beierkuhnlein C (2007) Biogeographie, Eugen Ulmer, Stuttgart.

Bel G, Hagberg A, Meron E (2012) Gradual regime shifts in spatially extended ecosystems. *Theoretical Ecology* **5**, 591-604.

Birand A, Howard DJ (2008) The relationship between proportion of endemics and species diversity on islands: expectations from a null model. *Ecography* **31**, 286-288.

Brown JH, Kodric-Brown A (1977) Turnover rates in insular biogeography-effects of immigration on extinction. *Ecology* **58**, 445-449.

Brown JH, Lomolino MV (2000) Concluding remarks: historical perspective and the future of island biogeography theory. *Global Ecology and Biogeography* **9**, 87-92.

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. *Ecology* **85**, 1771-1789.

Buhk C, Retzer V, Beierkuhnlein C, Jentsch A (2007) Predicting plant species richness and vegetation patterns in cultural landscapes using disturbance parameters. *Agriculture, Ecosystems and Environment* **122**, 446-452.

Bunnefeld N, Phillimore AB (2012) Island, archipelago and taxon effects: mixed models as a means of dealing with the imperfect design of nature's experiments. *Ecography* **35**, 15-22.

Cadena CD, Ricklefs RE, Jiménez I, Bermingham E (2005) Is speciation driven by species diversity? *Nature* **438**, E1-E2.

Carlquist S (1966) The biota of long-distance dispersal. I. Principles of dispersal and evolution. *Quarterly Review of Biology* **41**, 247-270.

Carnicer J, Brotons L, Sol D, Jordano P (2007) Community based processes behind species richness gradients: contrasting abundance-extinction dynamics and sampling effects in low- and high productivity areas. *Global Ecology and Biogeography* **16**, 709-719.

Carnicer J, Brotons L, Stefanescu C, Peñuelas J (2012) Biogeography of species richness gradients: linking adaptive traits, demography and diversification. *Biological Reviews* **87**, 457-479.

Carroll SP, Hendry AP, Reznick DN, Fox CW (2007) Evolution on ecological time-scales. *Functional Ecology* **21**, 387-393.

Carvalho JC, Cardoso P, Gomes P (2012) Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns. *Global Ecology and Biogeography* **21**, 760-771.

Chase JM (2010) Stochastic community assembly causes higher biodiversity in more productive environments. *Science* **328**, 1388-1391.

Chen X, He F (2009) Speciation and endemism under the model of island biogeography. *Ecology* **90**, 39-45.
Clark JS, Lewis M, Horvath L (2001) Invasion by extremes: population spread with variation in dispersal and reproduction. *The American Naturalist* **157**, 537–554.
Colwell RK, Rahbek C, Gotelli NJ (2004) The mid-domain effect and species richness patterns: What have we learned so far? *The American Naturalist* **163**, E1-E23.
Condit R, Pitman N, Leigh EG, Chave J, Terborgh J, Foster RB, Nunez P, Aguilar S, Valencia R, Villa G, Muller-Landau HC, Losos E, Hubbell SP (2002) Beta-diversity in tropical forest trees. *Science* **295**, 666-669.
Connor EF, McCoy ED (1979) The statistics and biology of the species-area relationship. *The American Naturalist* **113**, 791-833.
Connor SE, van Leeuwen JFN, Rittenour TM, van der Knaap WO, Ammann B, Björck S (2012) The ecological impact of oceanic island colonization - a palaeoecological perspective from the Azores. *Journal of Biogeography* **39**, 1007-1023.
Cordis News (2012) Exclusive species found at higher altitudes; http://cordis.europa.eu; RCN: 34496.
Coyne JA, Orr HA (2004) Speciation. Sinauer Associates, Sutherland.
Cramer MJ, Willig MR (2005) Habitat heterogeneity, species diversity and null models. *Oikos* **108**, 209-218.
Currie DJ, Mittelbach GG, Cornell HV, Field R, Guégan J-F, Hawkins BA, Kaufman DM, Kerr JT, Oberdorff T, O'Brien E, Turne JRG (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters* **7**, 1121-1134.
Dall SR, Bell AM, Bolnick DI, Ratnieks FL (2012) An evolutionary ecology of individual differences. *Ecology Letters* **15**, 1189-1198.
Darwin C (1859) The Origin of Species. Reprinted by Penguin Books, London.
Davies TJ, Savolainen V, Chase MW, Moat J, Barraclough TG (2004) Environmental energy and evolutionary rates in flowering plants. *Proceedings of the Royal Society B: Biological Sciences* **271**, 2195-2200.
Davis CC, Webb CO, Wurdack KJ, Jaramillo CA, Donoghue MJ (2005) Explosive radiation of Malpighiales supports a Mid-Cretaceous origin of modern tropical rain forests. *The American Naturalist* **165**, E36-E65.
De Nascimento L, Willis KJ, Fernández-Palacios JM, Criado C, Whittaker RJ (2009) The long-term ecology of the lost forests of La Laguna, Tenerife (Canary Islands). *Journal of Biogeography* **36**, 499-514.
Dengler J, Löbel S, Dolnik C (2009) Species constancy depends on plot size - a problem for vegetation classification and how it can be solved. *Journal of Vegetation Science* **20**, 754-766.
Dennis RLH, Hardy PB, Dapporto L (2012) Nestedness in island faunas: novel insights into island biogeography through butterfly community profiles of colonization ability and migration capacity. *Journal of Biogeography* **39**, 1412-1426.
Douda J, Doudová-Kochánková J, Boublík K, Drašnarová A (2012) Plant species coexistance at local scale in temperate swamp forest: test of habitat heterogeneity hypothesis. *Oecologia* **169**, 523-534.
Duivenvoorden JF, Svenning JC, Wright SJ (2002) Beta-diversity in tropical forests - response. *Science* **297**, 636.
Dullinger S, Willner W, Plutzar C, Englisch T, Schratt-Ehrendorfer L, Moser D, Ertl S, Essl F, Niklfeld H (2012) Post-glacial migration lag restricts range filling of plants in the European Alps. *Global Ecology and Biogeography* **21**, 829-840.
Duque Á, Phillips JF, von Hildebrand P, Posada CA, Prieto A, Rudas A, Suescún M, Stevenson P (2009) Distance decay of tree species similarity in protected areas on terra firme forests in Colombian Amazonia. *Biotropica* **41**, 599-607.
Ellers J, Kiers ET, Currie CR, McDonald BR, Visser B (2012) Ecological interactions drive evolutionary loss of traits. *Ecology Letters* **15**, 1071-1082.
Elton CS (1927) Animal Ecology. Sidgwick and Jackson, London.
Emerson BC, Kolm N (2005) Species diversity can drive speciation. *Nature* **434**, 1015-1017.
Essl F, Dullinger S, Plutzar C, Willner W, Rabitsch W (2011) Imprints of glacial history and current environment on correlations between endemic plant and invertebrate species richness. *Journal of Biogeography* **38**, 604-616.
Evans KL, Newson SE, Storch D, Greenwood JJ, Gaston KJ (2008) Spatial scale, abundance and the species-energy relationship in British birds. *Journal of Animal Ecology* **77**, 395-405.
Fattorini S (2010) The influence of geographical and ecological factors on island beta diversity patterns. *Journal of Biogeography* **37**, 1061-1070.
Fernández-Palacios JM, de Nascimento L, Otto R, Delgado JD, García-del-Rey E, Arévalo JR, Whittaker RJ (2011) A reconstruction of Palaeo-Macaronesia, with particular reference to the long-term biogeography of the Atlantic island laurel forests. *Journal of Biogeography* **38**, 226-246.
Fine PVA, Ree RH (2006) Evidence for a time-integrated species-area effect on the latitudinal gradient in tree diversity. *The American Naturalist* **168**, 796-804.
Forster G (1777) A Voyage Round the World, Vol. I (ed. by Thomas N & Berghof O, 2000). University of Hawai'i Press, Honolulu.
Francis AP, Currie DJ (2003) A globally consistent richness-climate relationship for angiosperms. *The American Naturalist* **161**, 523-536.
Franklin J, Keppel G, Webb EL, Seamon JO, Rey SJ, Steadman DW, Wiser SK, Drake DR (2012) Dispersal limitation, speciation, environmental filtering and niche differentiation influence forest tree communities in West Polynesia. *Journal of Biogeography* **in press**, doi: 10.1111/jbi.12038.
Fraser CI, Nikula R, Ruzzante DE, Waters JW (2012) Poleward bound: biological impacts of Southern Hemisphere glaciation. *Trends in Ecology and Evolution* **27**, 462-471.

Futuyma DJ (2009) Evolution. 2nd ed., Sinauer Associates, Sutherland.
Garcillán PP, Ezcurra E (2003) Biogeographic regions and beta-diversity of woody dryland legumes in the Baja California peninsula. *Journal of Vegetation Science* **14**, 859–868.
Gehrke B, Linder HP (2011) Time, space and ecology: why some clades have more species than other. *Journal of Biogeography* **38**, 1948-1962.
Giehl ELH, Jarenkow JA (2012) Niche conservatism and the differences in species richness at the transition of tropical and subtropical climates in South America. *Ecography* **35**, 933-943.
Gillespie RG (2006) Oceanic islands: models of diversity. In: Encyclopedia of Biodiversity (eds. Levin SA). Elsevier Ltd, Oxford.
Gillooly JF, Allen AP, Savage V-M, West GB (2004) Towards a metabolic theory of ecology. *Ecology* **85**, 1771-1789.
Givnish TJ (2010) Ecology of plant speciation. *Taxon* **59**, 1326-1366.
Gleason HA (1922) On the relation between species and area. *Ecology* **3**, 158-162.
Green JL, Holmes AJ, Westoby M, Oliver I, Briscoe D, Dangerfield M, Gillings M, Beattle AJ (2004) Spatial scaling of microbial eukaryote diversity. *Nature* **432**, 747-750.
Grinnell J (1908) The biota of the San Bernadino Mountains. *University of California publications in zoology* **5**, 1-170.
Grinnell J (1917) The niche-relationships of the California thrasher. *The Auk* **34**, 427-433.
Gruner DS, Gotelli N, Price J, Cowie RH (2008) Does species richness drive speciation? A reassessment with the Hawaiian biota. *Ecography* **31**, 279-285.
Guisan A, Rahbek C (2011) SESAM – a new framework integrating macroecological and species distribution models for predicting spatio-temporal patterns of species assemblages. *Journal of Biogeography* **38**, 1433-1444.
Gundale MJ, Fajardo A, Lucas RW, Nilsson M-C, Wardle DA (2011) Resource heterogeneity does not explain the diversity–productivity relationship across a boreal island fertility gradient. *Ecography* **34**, 887-896.
Habel JC, Zachos FE (2012) Past population history versus recent population decline – founder effects in island species and their genetic signatures. *Journal of Biogeography* **40**, 206-207.
Halas D, Zamparo D, Brooks DR (2005) A historical biogeographical protocol for studying biotic diversification by taxon pulses. *Journal of Biogeography* **32**, 249-260.
Heaney LR (2000) Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography. *Global Ecology and Biogeography* **9**, 59-74.
Heaney LR (2007) Is a new paradigm emerging for oceanic island biogeography? *Journal of Biogeography* **34**, 753-757.
Hewitt GM, Ibrahim KM (2001) Inferring glacial refugia and historical migrations with molecular phylogenies. In: Integrating Ecology and Evolution in a Spatial Context (eds Silvertown J, Antonovics J), pp. 97–123. Blackwell, Oxford.
Higgins SI, Nathan R, Cain ML (2003) Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? *Ecology* **84**, 1945-1956.
Hillebrand H (2004) On the generality of the latitudinal diversity gradient. *The American Naturalist* **163**, 192-211.
Holt RD (2009) Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences* **106**, 19659-19665.
Hortal J, Triantis KA, Meiri S, Thébault E, Sfenthourakis S (2009) Island species richness increases with habitat diversity. *The American Naturalist* **174**, 205-217.
Hortal J, Diniz-Filho JA, Bini LM, Rodríguez MÁ, Baselga A, Nogués-Bravo D, Rangel TF, Hawkins BA, Lobo JM (2011) Ice age climate, evolutionary constraints and diversity patterns of European dung beetles. *Ecology Letters* **14**, 741-748.
Hortal J (2012) Escaping the trap of low sample size in island biogeography. *Frontiers of Biogeography* **3**, 127-129.
Hubbell SP (2001) The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton.
Huston MA, DeAngelis DL (1994) Competition and coexistence the effects of resource transport and supply rates. *The American Naturalist* **144**, 954-977.
Hutchinson GE (1957) Concluding remarks. *Cold Spring Harbor Symposium* **22**, 415-427.
Hutchinson GE (1959) Homage to Santa-Rosalia or why are there so many kinds of animals? *The American Naturalist* **93**, 145-159.
Janzen DH (1967) Why mountain passes are higher in the tropics. *The American Naturalist* **101**, 233-249.
Jentsch A, Beierkuhnlein C (2003) Global Climate change and local disturbance regimes as interacting drivers for shifting altitudinal vegetation patterns. *Erdkunde* **57**, 216-231.
Jentsch A, Kreyling J, Elmer M, Gellesch E, Glaser B, Grant K, Hein R, Lara M, Mirzae H, Nadler S, Nagy L, Otieno DO, Pritsch K, Rascher U, Schädler M, Schloter M, Singh AP, Stadler J, Walter J, Wellstein C, Wöllecke J, Beierkuhnlein C (2011) Climate extremes initiate ecosystem regulating functions while maintaining productivity. *Journal of Ecology* **99**, 689-702.
Jentsch A, Steinbauer MJ, Alt M, Retzer V, Buhk C, Beierkuhnlein C (2012) A systematic approach to relate plant-species diversity to land use diversity across landscapes. *Landscape and Urban Planning* **107**, 236-244.
Jones MM, Tuomisto H, Clark DB, Olivas P (2006) Effects of mesoscale environmental heterogeneity and dispersal limitation on floristic variation in rain forest ferns. *Journal of Ecology* **94**, 181-195.
Jump AS, Huang T-J, Chou C-H (2012) Rapid altitudinal migration of mountain plants in Taiwan and its implications for high altitude biodiversity. *Ecography* **35**, 204-210.

Jurasinski G, Retzer V, Beierkuhnlein C (2009) Inventory, differentiation, and proportional diversity: a consistent terminology for quantifying species diversity. *Oecologia* **159**, 15-26.

Kallimanis AS, Panitsa M, Bergmeier E, Dimopoulos P (2011) Examining the relationship between total species richness and single island palaeo- and neo-endemics. *Acta Oecologica* **37**, 65-70.

Kalmar A, Currie DJ (2007) A unified model of avian species richness on islands and continents. *Ecology* **88**, 1309-1321.

Karger DN, Kluge J, Krömer T, Hemp A, Lehnert M, Kessler M (2011) The effect of area on local and regional elevational patterns of species richness. *Journal of Biogeography* **38**, 1177-1185.

Kiflawi M, Belmaker J, Brokovich E, Einbinder S, Holzman R (2007) Species diversity can drive speciation: comment. *Ecology* **88**, 2132-2135.

Kisel Y, Barraclough TG (2010) Speciation has a spatial scale that depends on levels of gene flow. *The American Naturalist* **175**, 316-334.

Kisel Y, McInnes L, Toomey NH, Orme CDL (2011) How diversification rates and diversity limits combine to create large-scale species –area relationships. *Philosophical Transactions of the Royal Society B: Biological Sciences* **366**, 2514-2525.

Kissling WD, Baker WJ, Balslev H, Barfod AS, Borchsenius F, Dransfield J, Govaerts R, Svenning J-C (2012) Quaternary and pre-Quaternary historical legacies in the global distribution of a major tropical plant lineage. *Global Ecology and Biogeography* **21**, 909-921.

Knope ML, Morden CW, Funk VA, Fukami T (2012) Area and the rapid radiation of Hawaiian Bidens (Asteraceae). *Journal of Biogeography* **39**, 1206-1216.

Körner C (2007) The use of "altitude" in ecological research. *Trends in Ecology and Evolution* **22**, 569-574.

Korhonen JJ, Soininen J, Hillebrand H (2010) A quantitative analysis of temporal turnover in aquatic species assemblages across ecosystems. *Ecology* **91**, 508-517.

Kraft NJ, Comita LS, Chase JM, Sanders NJ, Swenson NG, Crist TO, Stegen JC, Vellend M, Boyle B, Anderson MJ, Cornell HV, Davies KF, Freestone AL, Inouye BD, Harrison SP, Myers JA (2011) Disentangling the drivers of β diversity along latitudinal and elevational gradients. *Science* **333**, 1755-1758.

Kreft H, Jetz W, Mutke J, Kier G, Barthlott W (2008) Global diversity of island floras from a macroecological perspective. *Ecology Letters* **11**, 116-127.

Kreyling J, Jentsch A, Beierkuhnlein C (2011) Stochastic trajectories of succession initiated by extreme climatic events. *Ecology Letters* **14**, 758-764.

Kreyling J, Thiel D, Simmnacher K, Willner E, Jentsch A, Beierkuhnlein C (2012a) Geographic origin and past climatic experience influence the response to late spring frost in four common grass species in Central Europe. *Ecography* **35**, 268-275.

Kreyling J, Wiesenberg G, Huber G, Jentsch A, Konnert M, Thiel D, Walter J, Wohlfahrt C, Beierkuhnlein C (2012b) Cold hardiness of *Pinus nigra* Arnold as influenced by geographic origin, warming, and extreme summer drought. *Environmental and Experimental Botany* **78**, 99-108.

La Sorte FA, McKinney ML, Pyšek P, Klotz S, Rapson GL, Celesti-Grapow L, Thompson K, (2008) Distance decay of similarity among European urban floras: the impact of anthropogenic activities on beta-diversity. *Global Ecology and Biogeography* **17**, 363-371.

Lenoir J, Gegout JC, Guisan A, Vittoz P, Wohlgemuth T, Zimmermann NE, Dullinger S, Pauli H, Willner W, Grytnes JA, Virtanen RJ, Svenning JC (2010) Cross-scale analysis of the region effect on vascular plant species diversity in southern and northern European mountain ranges. *PLoS ONE* **5**, 1-13.

Lenoir J, Virtanen R, Oksanen J, Oksanen L, Luoto M, Grytnes J-A, Svenning J-C (2012) Dispersal ability links to cross-scale species diversity patterns across the Eurasian Arctic tundra. *Global Ecology and Biogeography* **21**, 851-860.

Le Roux PC, Virtanen R, Heikkinen RK, Luoto M (2012) Biotic interactions affect the elevational ranges of high-latitude plant species. *Ecography* **35**, 1048-1056.

Levin D (2006) Flowering phenology in relation to adaptive radiation. *Systematic Botany* **31**, 239-246.

Lewis MA (2000) Spread rate for a nonlinear stochastic invasion. *Journal of Mathematical Biology* **41**, 430-454.

Linder HP (2008) Plant species radiations: where, when, why? *Philosophical Transactions of the Royal Society B: Biological Sciences* **27**, 3097-3105.

Lira-Noriega A, Soberon J, Navarro-Siguenza AG, Nakazawa Y, Peterson TA (2007) Scale dependency of diversity components estimated from primary biodiversity data and distribution maps. *Diversity and Distribution* **13**, 185-195.

Lomolino M (2000a) A call for a new paradigm of island biogeography. *Global Ecology and Biogeography* **9**, 1-16.

Lomolino M (2000b) Ecology's most general, yet protean pattern: the species-area relationship. *Journal of Biogeography* **27**, 17-26.

Lomolino M (2001) Elevation gradients of species-density: historical and prospective views. *Global Ecology and Biogeography* **10**, 3-13.

Lomolino MV, Weiser MD (2001) Towards a more general species-area relationship: diversity on all islands, great and small. *Journal of Biogeography* **28**, 431-445.

Lomolino MV (2002) '...there are areas too small and areas too large to show clear diversity patterns...' R.H. MacArthur (1972: 191). *Journal of Biogeography* **29**, 555-557.

Lopes JS, Boessenkool S (2010) The use of approximate Bayesian computation in conservation genetics and its application in a case study on yellow-eyed penguins. *Conservation Genetics* **11**, 421-433.

Loreau M (2000) Are communities saturated? On the relationship between α, β and γ diversity. *Ecology Letters* **73**, 76.

Losos JB, Schluter D (2000) Analysis of an evolutionary species-area relationship. *Nature* **408**, 847-850.

Lundholm JT (2009) Plant species diversity and environmental heterogeneity: spatial scale and competing hypotheses. *Journal of Vegetation Science* **20**, 377-391.

MacArthur RH, Wilson EO (1963) An equilibrium theory of insular zoogeography. *Evolution* **17**, 373-387.

MacArthur RH, Wilson EO (1967) The Theory of Island Biogeography. Princeton University Press, Princeton, New York.

MacArthur RH (1972) Geographical ecology: patterns in the distribution of species. Harper & Row, New York.

Maiorano L, Cheddadi R, Zimmermann NE, Pellissier L, Petitpierre B, Pottier J, Laborde H, Hurdu BI, Pearman PB, Psomas A, Singarayer JS, Broennimann O, Vittoz P, Dubuis A, Edwards ME, Binney HA, Guisan A (2012) Building the niche through time: using 13000 years of data to predict the effects of climate change on three tree species in Europe. *Global Ecology and Biogeography* **22**, 302-317.

Mannion PD, Benson RBJ, Upchurch P, Butler RJ, Carrano MT, Barrett PM (2012) A temperate palaeodiversity peak in Mesozoic dinosaurs and evidence for Late Cretaceous geographical partitioning. *Global Ecology and Biogeography* **21**, 898-908.

McCain CM (2007) Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Global Ecology and Biogeography* **16**, 1-13.

McCain CM (2009) Global analysis of bird elevational diversity. *Global Ecology and Biogeography* **18**, 346-360.

McPeek MA, Brown JM (2007) Clade age and not diversification rate explains species richness among animal taxa. *The American Naturalist* **169**, 97-106.

Médail F, Diadema K (2009) Glacial refugia influence plant diversity patterns in the Mediterranean Basin. *Journal of Biogeography* **36**, 1333-1345.

Mergeay J, De Meester L, Eggermont H, Verschuren D (2011) Priority effects and species sorting in a long paleoecological record of repeated community assembly through time. *Ecology* **92**, 2267-2275.

Mittelbach GG, Schemske DW, Cornell HV, Allen AP, Brown JM, Bush MB, Harrison SP, Hurlbert AH, Knowlton N, Lessios HA, McCain CM, McCune AR, McDade LA, McPeek MA, Near TJ, Price TD, Ricklefs RE, Roy K, Sax DF, Schluter D, Sobel JM, Turelli M (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters* **10**, 315-331.

Monzón-Argüello C, Dell'Amico F, Moriniere P, Marco A, Lopez-Jurado LF, Hays GC, Scott R, Marsh R, Lee PLM (2012) Lost at sea: genetic, oceanographic and meteorological evidence for storm-forced dispersal. *Journal of the Royal Society Interface* **9**, 1725-1732.

Nekola JC, White PS (1999) The distance decay of similarity in biogeography and ecology. *Journal of Biogeography* **26**, 867-878.

Nekola JC, Brown JH (2007) The wealth of species: ecological communities, complex systems and the legacy of Frank Preston. *Ecology Letters* **10**, 188-196.

Nilsson SG, Bengtsson J, Ás S (1988) Habitat diversity or area per se? Species richness of woody plants, carabid beetles, and land snails on islands. *Journal of Animal Ecology* **57**, 685-704.

Nogales M, Heleno R, Traveset A, Vargas P (2012) Evidence for overlooked mechanisms of long-distance seed dispersal to and between oceanic islands. *New Phytologist* **194**, 313-317.

Nogué S, Rull V, Vegas-Vilarrúbia T (2012) Elevational gradients in the neotropical table mountains: patterns of endemism and implications for conservation. *Diversity and Distributions* **in press**, doi: 10.1111/ddi.12017.

Norberg J, Urban MC, Vellend M, Klausmeier CA, Loeuille N (2012) Eco-evolutionary responses of biodiversity to climate change. *Nature Climate Change* **2**, 747–751.

Olszewski TA (2004) A unified mathematical framework for the measurment of richness and evenness within and among multiple communities. *Oikos* **104**, 377-387.

Palmer MW (1994) Variation in species richness: towards a unification of hypotheses. *Folia Geobotanica et Phytotaxonomica* **29**, 511-530.

Palmer MW, White PS (1994) Scale dependence and the species-area relationship. *The American Naturalist* **144**, 717-740.

Panitsa M, Trigas P, Iatrou G, Sfenthourakis S (2010) Factors affecting plant species richness and endemism on land-bridge islands - an example from the East Aegean archipelago. *Acta Oecologica* **36**, 431-437.

Pau S, Gillespie TW, Wolkovich EM (2012) Dissecting NDVI–species richness relationships in Hawaiian dry forests. *Journal of Biogeography* **39**, 1678-1686.

Pereira HM, Proença VM, Vicente L (2007) Does species diversity really drive speciation? *Ecography* **30**, 328-330.

Presgraves DC (2010) The molecular evolutionary basis of species formation. *Nature Reviews Genetics* **11**, 175-180.

Preston FW (1960) Time and space and the variation of species. *Ecology* **41**, 611-627.

Preston FW (1962) Canonical distribution of commonness and rarity: Part 2. *Ecology* **43**, 410-432.

Qian H, Ricklefs RE (2011) Altitude, tree species diversity and the metabolic theory of ecology. *Global Ecology and Biogeography* **20**, 362-365.

Qian H, Ricklefs RE (2012) Disentangling the effects of geographic distance and environmental dissimilarity on global patterns of species turnover. *Global Ecology and Biogeography* **21**, 341-351.

Questad EJ, Foster BL (2008) Coexistence through spatio-temporal heterogeneity and species sorting in grassland plant communities. *Ecology Letters* **11**, 717-726.

Rabosky DL (2009) Heritability of Extinction Rates Links Diversification Patterns in Molecular Phylogenies and Fos-

sils. *Systematic Biology* **58**, 629-640.
Rapoport EH (1982) Areography. Geographical Strategies of Species. Translated by Drausal B, Pergamon Press, Oxford.
Reynolds HL, Mittelbach GG, Darcy-Hall TL, Houseman GR, Gross KL (2007) No effect of varying soil resource heterogeneity on plant species richness in a low fertility grassland. *Journal of Ecology* **95**, 723-733.
Ricklefs RE, Bermingham E (2002) The concept of the taxon cycle in biogeography. *Global Ecology and Biogeography* **11**, 353-361.
Ricklefs RE (2004) A comprehensive framework for global patterns in biodiversity. *Ecology Letters* **7**, 1-15.
Ricklefs RE (2006a) Evolutionary diversification and the origin of the diversity-environment relationship. *Ecology* **87**, 3-13.
Ricklefs RE (2006b) The unified neutral theory of biodiversity: Do the numbers add up? Ecology **87**, 1424-1431.
Ricklefs RE (2007) Estimating diversification rates from phylogenetic information. *Trends in Ecology and Evolution* **22**, 601-610.
Ricklefs RE (2010) Evolutionary diversification, coevolution between populations and their antagonists, and the filling of niche space. *Proceedings of the National Academy of Sciences* **107**, 1265-1272.
Ricklefs RE (2012) Naturalists, natural history, and the nature of biological diversity. The American Naturalist **179**, 423-435.
Rohde K (1992) Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* **65**, 514–527.
Rosenblum EB, Sarver BA, Brown JW, Des Roches S, Hardwick KM, Hether TD, Eastman JM, Pennell MW, Harmon LJ (2012) Goldilocks meets Santa Rosalia: An ephemeral speciation model explains patterns of diversification across time scales. *Journal of Evolutionary Biology* **39**, 255-261.
Rosenzweig ML (1995) Species Diversity in Space and Time. Cambridge University Press, New York.
Rosindell J, Phillimore AB (2011) A unified model of island biogeography sheds light on the zone of radiation. *Ecology Letters* **14**, 552-560.
Ruokolainen K, Tuomisto H (2002) Beta diversity in tropical forests - Response. *Science* **297**, 1439.
Salisbury CL, Seddon N, Cooney CR, Tobias JA (2012) The latitudinal gradient in dispersal constraints: ecological specialisation drives diversification in tropical birds. *Ecology Letters* **15**, 847-855.
Sanders NJ, Rahbek C (2012) The patterns and causes of elevational diversity gradients. *Ecography* **35**, 1-3.
Sarkar S, Margules C (2002) Operationalizing biodiversity for conservation planning. *Journal of Biosciences* **27**, 299-308.
Sax DF, Gaines SD, Brown JH (2002) Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. *The American Naturalist* **160**, 766-783.
Scheiner SM, Chiarucci A, Fox GA, Helmus MR, McGlinn DJ, Willig MR (2011) The underpinnings of the relationship between space, time, and species richness. *Ecological Monographs* **81**, 195-213.
Schemske DW, Mittelbach GG, Cornell HV, Sobel JM, Roy L (2009) Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology, Evolution, and Systematics* **40**, 245-269.
Schmera D, Podani J (2011) Comments on separating components of beta diversity. *Community Ecology* **12**, 153-160.
Schmiedinger A, Kreyling J, Steinbauer MJ, Macdonald E, Jentsch A, Beierkuhnlein C (2012) A continental comparison indicates long-term effects of forest management on understory diversity in coniferous forests. *Canadian Journal of Forest Research* **42**, 1239-1252.
Schneeweiss GM, Schönswetter P (2010) The wide but disjunct range of the European mountain plant *Androsace lactea* L. (Primulaceae) reflects Late Pleistocene range fragmentation and post-glacial distributional stasis. *Journal of Biogeography* **37**, 2016-2025.
Schnitzler J, Graham CH, Dormann CF, Schiffers K, Peter LH, Higgins S (2012) Climatic niche evolution and species diversification in the Cape flora, South Africa. *Journal of Biogeography* **39**, 2201-2211.
Sekercioglu CH, Daily GC, Ehrlich PR (2004) Ecosystem consequences of bird declines. *Proceedings of the National Academy of Sciences* **101**, 18042-18047.
Sepkoski JJ (1998) Rates of speciation in the fossil record. *Philosophical Transactions of the Royal Society B: Biological Sciences* **353**, 315-326.
Sfenthourakis S, Panitsa M (2012) From plots to islands: species diversity at different scales. *Journal of Biogeography* **39**, 750-759.
Soberón J (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters* **10**, 1115-1123.
Soininen J, McDonald R, Hillebrand H (2007) The distance decay of similarity in ecological communities. *Ecography* **30**, 3-12.
Soininen J (2010) Species turnover along abiotic and biotic gradients: Patterns in space equal patterns in time? *BioScience* **60**, 433-439.
Stegen JC, Freestone AL, Crist TO, Anderson MJ, Chase JM, Comita LS, Cornell HV, Davies KF, Harrison SP, Hurlbert AH, Inouye BD, Kraft NJB, Myers JA, Sanders HJ, Swenson NG, Vellend M (2012) Stochastic and deterministic drivers of spatial and temporal turnover in breeding bird communities. *Global Ecology and Biogeography*, **22**, 202-212.
Steinbauer MJ (2009) The moving target - measuring biological diversity. Master thesis at the University of Bayreuth.
Stephens PR, Wiens JJ (2003) Explaining species richness from continents to communities: the time-for-speciation effect in emydid turtles. *The American Naturalist* **161**, 112-128.

Stevens GC (1989) The latitudinal gradients in geographical range: how so many species co-exist in the tropics. *The American Naturalist* **133**, 240-256.
Storch D, Gaston KJ (2004) Untangling ecological complexity on different scales of space and time. *Basic and Applied Ecology* **5**, 389-400.
Strunz S (2012) Is conceptual vagueness an asset? Arguments from philosophy of science applied to the concept of resilience. *Ecological Economics* **76** 112-118.
Stuessy TF, Jakubowsky G, Gómez RS, Pfosser M, Schlüter PM, Fer T, Sun BY, Kato H (2006) Anagenetic evolution in island plants. *Journal of Biogeography* **33**, 1259-1265.
Stuessy TF, Takayama K, Sepúlveda PL (2012) Founder effects are invisible in endemic species of oceanic islands. J*ournal of Biogeography* **39**, 1565-1566.
Sutherland C, Elston DA, Lambin X (2012) Multi-scale processes in metapopulations: contributions of stage structure, rescue effect, and correlated extinctions. *Ecology* **93**, 2465-2473.
Svenning J-C (2001) On the Role of Microenvironmental Heterogeneity in the Ecology and Diversification of Neotropical Rain-Forest Palms (Arecaceae). *The Botanical Review* **67**, 1-53.
Svenning J-C, Skov F (2007) Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? *Ecology Letters* **10**, 453-460.
Svensson JR, Lindegarth M, Jonsson PR, Pavia H (2012) Disturbance-diversity models: what do they really predict and how are they tested? *Proceedings of the Royal Society B; Biological Sciences* **279**, 2163–2170.
Swenson NG, Enquist BJ, Pither J, Kerkhoff AJ, Boyle B, Weiser MD, Elser JJ, Fagan WF, Forero-Montana J, Fyllas N, Kraft NJB, Lake JK, Moles AT, Patino S, Phillips OL, Price CA, Reich PB, Quesada CA, Stegen JC, Valencia R, Wright IJ, Wright SJ, Andelman S, Jorgensen PM, Lacher TE, Monteagudo A, Nunez-Vargas P, Vasquez R, Nolting KM (2012) The biogeography and filtering of woody plant functional diversity in North and South America. *Global Ecology and Biogeography* **21**, 798-808.
Tamme R, Hiiesalu I, Laanisto L, Szava-Kovats R, Pärtel M (2010) Environmental heterogeneity, species diversity and co-existence at different spatial scales. *Journal of Vegetation Science* **21**, 796-801.
Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* **31**, 79–92.
Thornton IWB, Zann RA, Rawlinson PA, Tidemann CR, Adikerana AS, Widjoya HT (1988) Colonization of the Krakatau Islands by vertebrates: Equilibrium, succession, and possible delayed extinction. *Proceedings of the National Academy of Sciences* **85**, 515-518.
Tilman D, Pacala S (1993) The maintenance of species richness in plant communities. In: Species diversity of ecological communities: historical and geographical perspectives. (eds Ricklefs RE, Schluter D), pp 13–25. University of Chicago Press, Chicago.
Tjørve E (2009) Shapes and functions of species-area curves (II): a review of new models and parameterizations. *Journal of Biogeography* **36**, 1435-1445.
Triantis KA, Mylonas M, Whittaker RJ (2008a) Evolutionary species-area curves as revealed by single-island endemics: insights for the inter-provincial species-area relationship. *Ecography* **31**, 401-407.
Triantis KA, Nogués-Bravo D, Hortal J, Borges AVP, Adsersen H, Fernández -Palacios JM, Araújo MB, Whittaker RJ (2008b) Measurements of area and the (island) species–area relationship: new directions for an old pattern. *Oikos* **117**, 1555-1559.
Triantis KA, Guilhaumon F, Whittaker RJ (2012a) The island species-area relationship: biology and statistics. *Journal of Biogeography* **39**, 215-231.
Triantis KA, Hortal J, Amorim I, Cardoso P, Santos AMC, Gabriel R, Borges PAV (2012b) Resolving the Azorean knot: a response to Carine & Schaefer (2010). *Journal of Biogeography* **39**, 1179-1184.
Tscharntke T, Tylianakis JM, Rand TA, Didham RK, Fahrig L, Batáry P, Bengtsson J, Clough Y, Crist TO, Dormann CF, Ewers RM, Fründ J, Holt RD, Holzschuh A, Klein AM, Kleijn D, Kremen C, Landis DA, Laurance W, Lindenmayer D, Scherber C, Sodhi N, Steffan-Dewenter I, Thies C, van der Putten WH, Westphal C (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews of the Cambridge Philosophical Society* **87**, 661-685.
Tuomisto H, Ruokolainen K, Yli-Halla M (2003) Dispersal, environment, and floristic variation of western Amazonian forests. *Science* **299**, 241-244.
Uddin M, Steinbauer MJ, Beierkuhnlein C (2011) Stand characteristics and spatial species aggregation in a Bangladesh forest ecosystem. *Diversity* **3**, 453-465.
Ulrich W, Almeida-Neta M (2012) On the meaning of nestedness: back to the basics. *Ecography* **35**, 865-871.
Urban MC, De Meester L (2009) Community monopolization: local adaptation enhances priority effects in an evolving metacommunity. *Proceedings of the Royal Society B -Biological Sciences* **276**, 4129-4138.
Van Valen L (1973) "A New Evolutionary Law". *Evolutionary Theory* **1**, 1-30.
Verzijden MN, Cate C, Servedio MR, Kozak GM, Boughman JW, Svensson EI (2012) The impact of learning on sexual selection and speciation. *Trends in Ecology and Evolution* **27**, 511-519.
Vilenkin BY, Chikatunov VI, Coad BW, Schileyko AA (2009) A random process may control the number of endemic species. *Biologia* **64**, 107-112.
Vitousek PM (2002) Oceanic islands as model systems for ecological studies. *Journal of Biogeography* **29**, 573-582.
Wallace AR (1878) Tropical Nature and Other Essays. Macmillan, New York.
Walter J, Beierkuhnlein C, Jentsch A, Kreyling J (2012) Ecological stress memory and cross stress tolerance in plants

in the face of climate extremes. *Environmental and Experimental Botany* **in press**, doi: 10.1016/j.envexpbot.2012.02.009.
Waters JM (2011) Competitive exclusion: phylogeography's "elephant in the room"? *Molecular Ecology* **20**, 4388-4394.
Watson HC (1835) Remarks on the Geographical Distribution of British Plants: Chiefly in Connection with Latitude, Elevation, and Climate. Longman, Rees, Orme, Brown, Green, and Longman, London.
Weir JT, Schluter D (2007) The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science* **315**, 1574-1576.
West GB, Brown JH (2005) The origin of allometric scaling laws in biology from genomes to ecosystems: towards a quantitative unifying theory of biological structure and organization. *Journal of Experimental Biology* **208**, 1575-1592.
White EP, Ernest SKM, Adler PB, Hurlbert AH, Lyons SK (2010) Integrating spatial and temporal approaches to understanding species richness. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 3633-3643.
Whitehead DR, Jones CE (1969) Small islands and the equilibrium theory of insular biogeography. *Evolution* **23**, 171-179.
Whittaker RH (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* **30**, 280–338.
Whittaker RH (1967) Gradient analysis of vegetation. *Biological Reviews* **42**, 207-264.
Whittaker RH (1972) Evolution and measurement of species diversity. *Taxon* **21**, 213-251.
Whittaker RJ, Bush MB, Richards K (1989) Plant recolonization and vegetation succession on the Krakatau Islands, Indonesia. *Ecological Monographs* **59**, 59-123.
Whittaker RJ (2000) Scale, succession and complexity in island biogeography: are we asking the right questions? *Global Ecology and Biogeography* **9**, 75-85.
Whittaker RJ, Willis KJ, Field R (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography* **28**, 453-470.
Whittaker RJ, Ladle RJ, Araújo MB, Fernández-Palacios JM, Delgado JD, Arevalo JR (2007) The island immaturity - speciation pulse model of island evolution: an alternative to the "diversity begets diversity" model. *Ecography* **30**, 321-327.
Whittaker RJ, Fernández-Palacios JM (2007) Island Biogeography: Ecology, Evolution, and Conservation. 2nd edition. Oxford University Press, Oxford.
Whittaker RJ, Triantis KA, Ladle RJ (2008) A general dynamic theory of oceanic island biogeography. *Journal of Biogeography* **35**, 977-994.
Whittaker RJ, Triantis KA, Ladle RJ (2010) A general dynamic theory of oceanic island biogeography: extending the MacArthur-Wilson theory to accommodate the rise and fall of volcanic islands. In: The Theory of Island Biogeography Revisited (eds Losos JB, Ricklefs RE), pp. 88-115. Princeton University Press, Princeton.
Wiens JJ, Donoghue MJ (2004) Historical biogeography, ecology and species richness. *Trends in Ecology and Evolution* **19**, 639-644.
Wiens JJ, Parra-Olea G, García-París M, Wake DB (2007) Phylogenetic history underlies elevational biodiversity patterns in tropical salamanders. *Proceedings of the Royal Society Series B: Biological Sciences* **274**, 919-928.
Wiens JJ, Ackerly DD, Allen AP, Anacker BL, Buckley LB, Cornell HV, Damschen EI, Davies TJ, Grytnes JA, Harrison SP, Hawkins BA, Holt RD, McCain CM, Stephens PR (2010) Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* **13**, 1310-1324.
Williamson M, Gaston KJ, Lonsdale WM (2001) The species-area relationship does not have an asymptote! *Journal of Biogeography* **28**, 827-830.
Wilson EO (1959) Adaptive shift and dispersal in a tropical ant fauna. *Evolution* **13**, 122-144.
Wilson EO (1961) The nature of the taxon cycle in the Melanesian ant fauna. *The American Naturalist* **95**, 169-193.
Winter M, Kühn I, La Sorte FA, Schweiger O, Nentwig W, Klotz S (2010) The role of non-native plants and vertebrates in defining patterns of compositional dissimilarity within and across continents. *Global Ecology and Biogeography* **19**, 332–342.
Witt CC, Maliakal-Witt S (2007) Why are diversity and endemism linked on islands? *Ecography* **30**, 331-333.
Wright DH (1983) Species-energy theory, an extension of species-area theory. *Oikos* **41**, 496-506.
Yule GU (1924) A mathematical theory of evolution, based on the conclusions of Dr J. C. Willis. *Philosophical Transactions of the Royal Society B: Biological Sciences* **213**, 21-87.
Zöller L, von Suchodoletz H, Küster N (2003) Geoarchaeological and chronometrical evidence of early human occupation on Lanzarote (Canary Islands). *Quaternary Science Reviews* **22**, 1299-1307.
Zöller L, von Suchodoletz H, Blanchard H, Faust D, Hambach U (2004) Response to the "Comment on 'Geoarchaeological and chronometrical evidence ...' " by J.C. Carracedo et al. (Quaternary Science Reviews 23, 2045-2049). *Quaternary Science Reviews* **23**, 2049-2052.

2. Manuscript 1 - Current measures for distance decay in similarity of species composition are influenced by study extent and grain size

Global Ecology and Biogeography 21 (2012) DOI: 10.1111/j.1466-8238.2012.00772.x

Manuel Jonas Steinbauer[1*], Klara Dolos[2], Björn Reineking[2], Carl Beierkuhnlein[1]

[1] Dept. of Biogeography, BayCEER, University of Bayreuth, D-95447 Bayreuth, Germany
[2] Biogeographical Modelling, BayCEER, University of Bayreuth, D-95447 Bayreuth, Germany
* Corresponding author: Manuel.Steinbauer@uni-bayreuth.de

ABSTRACT
Aim: The relationship between geographic distance and similarity in species composition is regularly used as a measure of species turnover and beta diversity. Distance decay analyses are applied, cited and compared despite variable extent, and different grain sizes of records (e.g. plots, islands, states) are regularly used within such analyses. Currently, differences among distance decay relationships that cover different grain sizes and extents are attributed to ecological processes that are suspected to operate differently over varying extent and grain size. We assess whether the implicit assumption that the distance decay relation is independent from grain size and study extent is valid, or whether sampling design could be the underlying cause for observed differences.
Location: An artificial one-dimensional "landscape".
Methods: The distance decay relationship was quantified in simulated communities. Grain and study extent were varied systematically. In each sampled data set the linear relation of Simpson and Sørensen similarity to geographic distance (on both a log-transformed and the original scale) between 100 even sized equidistant plots was assessed using linear regression and generalized linear regression with log-link function. Regressions were applied either including or removing zero similarities from the data.
Results: Both, slope (measuring turnover) and goodness of fit measure r^2 (quantifying the influence of space on species composition) of the distance decay relationship were strongly influenced by grain and study extent. Approaches that are able to cope with zero similarity values of large distance comparisons were less dependent on grain and extent.
Main conclusions: Reported differences between landscapes detected by current distance decay measures cannot be explicitly traced back to ecological scale-specific processes. Instead, they can largely be attributed to sampling design and are highly sensitive to grain size and study extent. More appropriate approaches for the study of distance decay and the understanding of scale specific processes are required.

KEYWORDS: beta diversity, biodiversity, ecological gradient, macroecology, dissimilarity, scale dependence, Simpson similarity, Sørensen similarity, species turnover

INTRODUCTION

Dependence on grain and extent is a widely observed phenomenon for species richness patterns (e.g. Arrhenius, 1921; Palmer & White, 1994; Beierkuhnlein, 1998; Lira-Noriega *et al.*, 2007; Dengler *et al.*, 2009). Aggregated beta diversity indices (Whittaker's beta or mean Simpson similarity) have been found to be grain dependent (Kallimanis *et al.*, 2008). However, a systematic assessment of the influence of sampling grain and extent on similarity and, in particular, on the frequently applied distance decay relationship is needed. In ecology 'distance decay' denotes the phenomenon of a decline in similarity in community assembly with increasing spatial distance. The decay of similarity in species composition with distance measures the "*variation or rate in species turnover*" (Soininen 2010).

Various empirical case studies have indicated that the distance decay relation may vary with study extent (Maloney & Munguia, 2011; Martiny *et al.*, 2011; Soininen *et al.*, 2011) and grain size (Girdler & Barrie, 2008). It has been suggested that scale dependence of dispersal-driven assembly as well as environmental filters are the major causes of the observed phenomenon (Soininen *et al.*, 2007; Girdler & Barrie, 2008; Maloney & Munguia, 2011; Martiny *et al.*, 2011; Soininen *et a*l, 2011).

In contrast, we suspect that not only ecological reasons are behind the observed differences in the distance decay between studies of different extent and grain size, but that sampling design has a considerable influence, too. Empirical studies are of limited value when investigating this methodological problem. The underlying relationships of real data are unknown. Simulated data enable to work on a well-defined spatial setting of ecological objects (e.g. distribution of species) and systematically vary the sampling design (Zurell et al. 2010). To our knowledge a simulation-based assessment of distance decay measures is still lacking. However, such an assessment can be seen as a crucial prerequisite for meta-analyses integrating different empirical studies.

A decline in similarity with distance was detected within a multitude of complex systems in geography, sociology and economy (Nekola & Brown, 2007). Classic studies as Whittaker (1960, 1972) and Preston (1962) already mention the phenomenon. However, it was the publication of Nekola & White (1999) that placed distance decay at the focus of ecological research. Especially high interest in the phenomenon was shown by studies on tropical ecosystems (Condit *et al.*, 2002; Duivenvoorden *et al.*, 2002; Ruokolainen & Tuomisto, 2002; Tuomisto *et al.*, 2003; Green *et al.*, 2004). More recently, changes in species composition along temporal gradients (temporal turnover) are of increased focus in ecological research (Korhonen *et al.*, 2010; Soininen, 2010; Kreyling *et al.*, 2011).

The distance decay relation is used to quantify the effect of geography (e.g. in relation to environmental differences; Steinitz *et al.*, 2005) and has been suggested as a valuable tool for the understanding of species assemblages (Morlon *et al.*, 2008). If used appropriately the distance decay relation is proposed as a powerful tool for testing mechanistic ecological theories (Chave & Leigh, 2002; Condit *et al.*, 2002).

Currently the main explanations for a decline in community similarity with distance are (1) gradual changes in the environment, (2) structural properties of the landscape limiting dispersal, and (3) random spatially correlated processes (Soininen *et al.*, 2007).

The first explanation states that species distribution reflects the environment mainly composed of climate, soil properties and abundant biota. The adaptation of species to ecological niches provides the basis for a pattern where species assemblages follow a decline in environmental similarity with distance (Nekola & White, 1999; Tuomisto *et al.*, 2003). The second explanation refers to structural properties of landscapes such as transmissibility, which modify the dispersal rates of individuals. Consequently the decrease in similarity with distance is higher in more fragmented landscapes (Garcillán & Ezcurra, 2003). The third explanation is related to the second, but with a more general scope. It has been shown that even random dispersal or speciation can create local patterns and thus produce a decline in similarity with distance without the necessity of environmental dissimilarities (Hubbell, 2001; Soininen *et al.*, 2007). A theoretical framework on the distance decay relationship has been developed illustrating that it is influ-

enced by the species-specific aggregation of populations and by the matrix-specific species-abundance distributions in landscapes (Morlon *et al.*, 2008).

The majority of assessments on spatial decay of community similarity considered a continental or intercontinental extent (e.g. McKinney, 2004; Qian *et al.*, 2009; Krasnov *et al*, 2010). Studies with a spatial extent below 10 km are rare. Jones *et al.* (2006), Girdler & Barrie (2008) and Hassler *et al.* (2010), however, identified a rapid decline of similarity in species composition with distance, also for extents of less than 10 km (see table A1 for an overview of studies focussing on plants).

The understanding of ecosystems and their determining processes could be improved by comparing the decline in similarity with changing distance. Studies attempting to draw conclusions from such comparisons considered distance decay studies of extents different to their own, implicitly assuming scale independence (e.g. Jones *et al.*, 2006, Duque *et al.*, 2009; Lenoir *et al.*, 2010). Furthermore, distance decay studies are frequently applied on samples of different grain size (plot size; such as islands or states; e.g. La Sorte *et al.*, 2008; Fattorini, 2010; Steinbauer & Beierkuhnlein, 2010; Winter *et al.*, 2010) implicitly assuming that the distance decay relation is independent of grain size. A quantitative meta-analysis of Soininen *et al.* (2007) comprising 401 different distance decay relations provided indications that the strength of distance decay in similarity strongly depends on the group of organisms as well as on the region under study. Other studies also found extent-dependencies, which were interpreted as ecological processes operating on different scales (Soininen *et al.*, 2007; Girdler & Barrie, 2008; Maloney & Munguia, 2011; Martiny *et al.*, 2011; Soininen *et al.*, 2011).

Whether or not the scale dependence of current distance decay measures can be attributed to ecological processes or finally should be recognized as a mathematical artefact (see considerations in Nekola & White, 1999), has, until now, not been consistently tested. Here, we employed simulation studies based on artificial data in order to investigate the interaction of the distance decay relation with spatial extent, grain size (represented by the plot size) and the actually variable of interest, i.e. species turnover. A one-dimensional "landscape" was simulated and standard distance decay analyses were applied.

METHODS

To assess distance decay it has been suggested to calculate the dissimilarity between all pairs of records (plots, sites) within a data set (e.g. Nekola & White, 1999; Jurasinski *et al.,* 2009, Astorga *et al.*, 2011). A linear regression is employed with spatial distance between pairs as independent and dissimilarity as dependent variable. The slope of the distance decay relationship has been suggested as a measure of beta diversity (Jurasinski et al., 2009). A log-transformation of similarity, distance or both variables is occasionally suggested to account for the range limits of common similarity indices (e.g. Sørensen and Simpson index) between zero and one, or for an exponential decline of similarity with distance, respectively. To test model performance and significance, pseudoreplication has to be accounted for. One possible solution is the use of permutation tests.

We aimed to test different distance decay measures systematically by varying grain size and study extent for the simplest setting possible, i.e. an isotropic one-dimensional landscape. If the distance decay measurement is not able to detect the underlying spatial pattern consistently in a simplified landscape, it is unlikely to do so in more realistic landscapes where additional processes and noise influence species distributions.

This simplified one-dimensional landscape with a length of 30,000 units hosted 1000 species each characterized by a normal distribution ($N(\mu_i, \sigma_i^2)$), defining the probability of occurrence for each location, where μ_i represents the mean, i.e the centre of the i-th species' distribution, and σ_i represents the standard deviation, i.e. the range of the distribution. A large standard deviation resulted in a larger distribution range of species. The centres of the species distributions were placed evenly spaced in the landscape; the standard deviation was set equal for all species within one landscape.

From each species distribution, 1000 individuals were randomly drawn and placed in the landscape (Fig. 1a). Sampling was only done within the centred 10,000 landscape units (out of 30,000) in order to minimise edge effects. Continuous units of a specific study extent were taken from a random position within these 10,000 landscape units (Fig A1). The sampling procedure placed 100 even sized equidistant survey plots over the study extent. Each plot covered one unit. To increase plot size representing the grain size by one, a plot sampled from the same landscape unit (location) in a second newly simulated landscape (with the same species properties) was merged with the first plot. This corresponds to an increase in plot size perpendicular to the landscape gradient, i.e. the shape of larger plots became rectangular rather than quadratic. This enabled us to keep inter plot distance constant while increasing plot size (Fig. 1b). A presence-absence record was taken for each species in each plot.

The distance decay relation was assessed using Simpson similarity (Lennon *et al.*, 2001 based on Simpson, 1943) and Sørensen similarity (Sørensen, 1948 based on Dice, 1945). Simpson similarity measures species turnover and is said to be independent from richness gradients (Baselga, 2010). Thus the fact of larger plots having higher chances to host more species should not affect the analysis. In contrast, Sørensen similarity combines species turnover and nestedness in one similarity measure (Baselga, 2010). Simpson and Sørensen similarity are among the most often used indices for distance decay studies. Distance decay relations for the artificial landscape were calculated with untransformed and log-transformed similarity index and/or spatial distance (e.g. Nekola & White, 1999). Untransformed relations are problematic as the fitted line intersects with the x-axis as well as with the y-axis implying negative similarity values after a certain distance and negative distances for specific similarity values (Uddin et al. 2011). However, it has the advantage of a straightforward interpretation within the range of admissible values for similarity and distance. It appears that most studies of distance decay in ecology apply non-transformed relations. However, as all possible combination of log-transformed and untransformed values of similarity and distance are being used, we applied all of them on the simulated data. The log-transformation of similarity values incurs the problem of log(0) being non-finite. Nekola & White (1999) thus removed all comparisons with zero similarity from their data. They argued that similarity falls to zero at some distance and is afterwards independent of distance. Millar *et al.* (2011) point out that this justification is not valid if pairs with zero-similarity in species composition have the same or even a shorter Euclidean distance than pairs of sites that have considerable species overlap, a situation that is rather common. Other authors simply did not specify how they cope with the problem, presumably as they did not face the problem (Qian, 2008, 2009; Martiny *et al.*, 2011). Here we tested three different approaches to solve the problem. First, we applied log(x+1) transformation on similarity values, as it is the most common way to deal with zeros in log-transformations, although other constants than 1 may be more appropriate in many cases (see e.g. Williams *et al.*, 2009). More generally, we note that log-transformation of observed values that may contain zeros is often problematic, irrespective of the particular constant that is used to deal with zeros (Wilson 2007). Secondly, we followed Nekola & White (1999) and removed all comparisons with zero similarity from the data before calculating the distance decay. Thirdly, as suggested by Millar *et al.* (2011), we applied generalized linear models (GLM) with a log link function. This approach also models the logarithm of similarity values as a linear function of distance, but does not require an explicit log-transformation of the observed similarity values. Other error distributions than the binomial one suggested by Millar *et al.* (2007), e.g. Gaussian, may be chosen and combined with a log link function. Since we found that the results using either error distribution were very similar, we present only results for the Gaussian one.

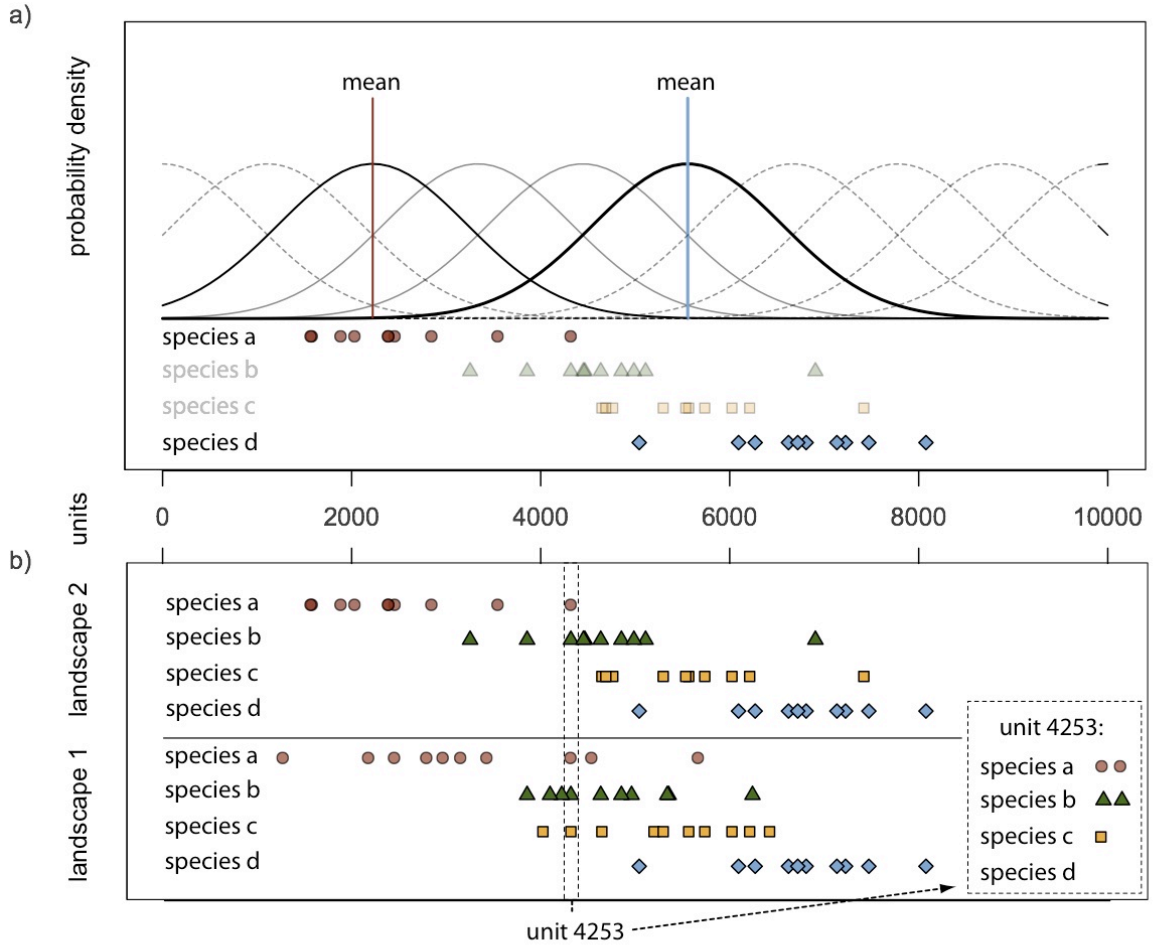

Figure 1: *a) Species (here only a subset) were evenly placed along the 30,000 units. The standard deviation of a species' distribution is responsible for the degree of species turnover. Species standard deviations were set to 100, 500, 1000, or 5000. Of each species, 1000 individuals where randomly placed in the one-dimensional landscape according to their distribution; for each combination of grain and extent, 1000 replicates were produced. b) To keep plot distance constant while increasing plot size, two ore more landscapes where sampled, i.e. plots sizes were increased perpendicular to the landscape gradient. Plots covered the same location in all landscapes (two are shown here).*

In sum, we compared 24 approaches to assess distance decay: untransformed similarity values (with/without removing of zero similarities), log(x+1)/log(x) transformation (with/without removing of zero similarities), GLM (with/without removing of zero similarities); each of these six approaches was applied to untransformed and log-transformed spatial distances, and to both Simpson and Sørensen similarity. For each approach, plot size was modified from 1 to 20 units (in 20 equidistant steps), extent from 100 to 10,000 landscape units (in steps of 100 until 1000 and of 500 afterwards) and species standard deviation from 100 to 5000 (in levels of 100, 500, 1000 and 5000), resulting in 2240 parameter combinations. For each combination 1000 replicates were simulated to account for stochasticity. Turnover in species composition is the target variable of distance decay studies (Anderson *et al.*, 2011). The controlling variable for the decline in similarity of species composition with distance between survey plots is – in the artificial data set – the species' standard deviations. The slope of the distance decay line should become steeper with a decline in standard deviation of species. Quantifying differences in species standard deviations of the simulated landscapes thus was the challenge the distance decay measures had to meet. An effective measure for the distance decay relation should have a monotonous relationship with species standard deviations and a narrow statistical spread. The

measure should only depend on the species distribution properties and, if not entirely avoidable, only weakly on the sampling procedure. All calculations were performed in R (R Development Core Team, 2010; packages: simba 0.2-5 from Jurasinski, 2007; vegan 1.17-0 from Oksanen et al. 2010).

RESULTS

The slope of the distance decay relation depended on study extent, grain size and species standard deviation (Fig. 2). This held true for all investigated similarity measures and transformation combinations (Fig. A2 and A3 in Appendix). The observed pattern scaled with the standard deviations of the species' distribution. To visualise the interaction of study extent and grain size a species standard deviation of 500 appeared to be optimal (Fig. 2b). Simulations with substantially higher or lower species standard deviations (Fig. 2 a, c, d) covered only parts of the potential patterns.

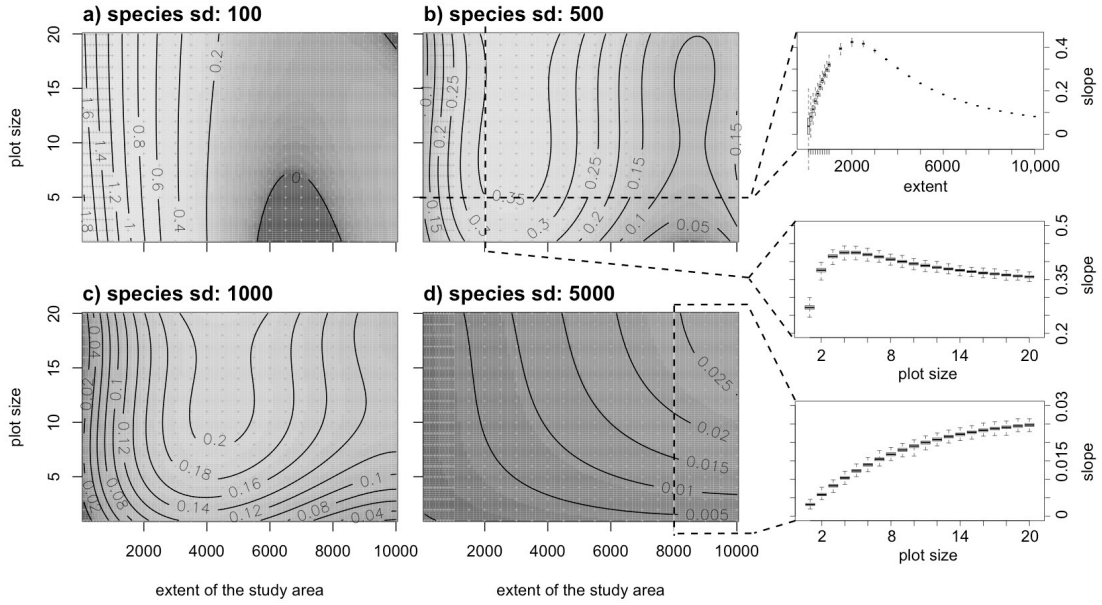

Figure 2: *Variation in slope with a change in plot size and study extent for four different species characteristics (standard deviation 100, 500, 1000 and 5000; Simpson similarity, linear regression with zero similarities and untransformed variables). Plot size and slope is measured in artificial units. Slope represents the median of 1000 replicates and was multiplied with -1000 to improve visualisation*

For untransformed and log-transformed similarity and /or distance values, the range of calculated slopes covered more than one order of magnitude. The slope of the distance decay relation (slope of the regression line) increased with increasing species standard deviation in the range of small extents and declined after reaching a point of maximum slope at about 4 species standard deviations, representing 95% species turnover. After this point, differences between slopes decreased with increasing extent. Extent influenced the slope considerably stronger than grain size (Fig. 2b). The generalized linear models with a log link function exhibited a different pattern: Here, the slope continuously increased with increasing extent (Fig. 3, 4c, d and A2). Overall, while there remained substantial dependence of slope on study extent (up to an order of magnitude), this approach was the least affected by study extent and nearly independent from a change in plot size (Fig. 4c, d and A2).

The explanatory power of the model, indicated by r^2, varied between 0 (no explanatory power) and 1 (all variation explained) depending on grain size and study extent. For the effect of extent, r^2 followed the pattern of slope with an optimum at about 4 species standard deviations, but r^2 increased monotonously with plot size (Fig. 5, only analyzed for linear models).

In addition to the interaction of slope with study extent and grain size, we assessed the potential of the distance decay relationship to indicate the target variable "species turnover", i.e. the species distribution's standard deviation. As an example, the relation of species standard deviations and slope of the regression line is shown for untransformed Simpson similarity and spatial distance (Fig. 3). When zeros were not removed from the data before calculating the distance decay relation, differences in species standard deviation could not be clearly separated (Fig. 3a). Removing zeros from the data led to a better-defined relation (Fig. 3b and A2) and especially improved the dependency of grain size.

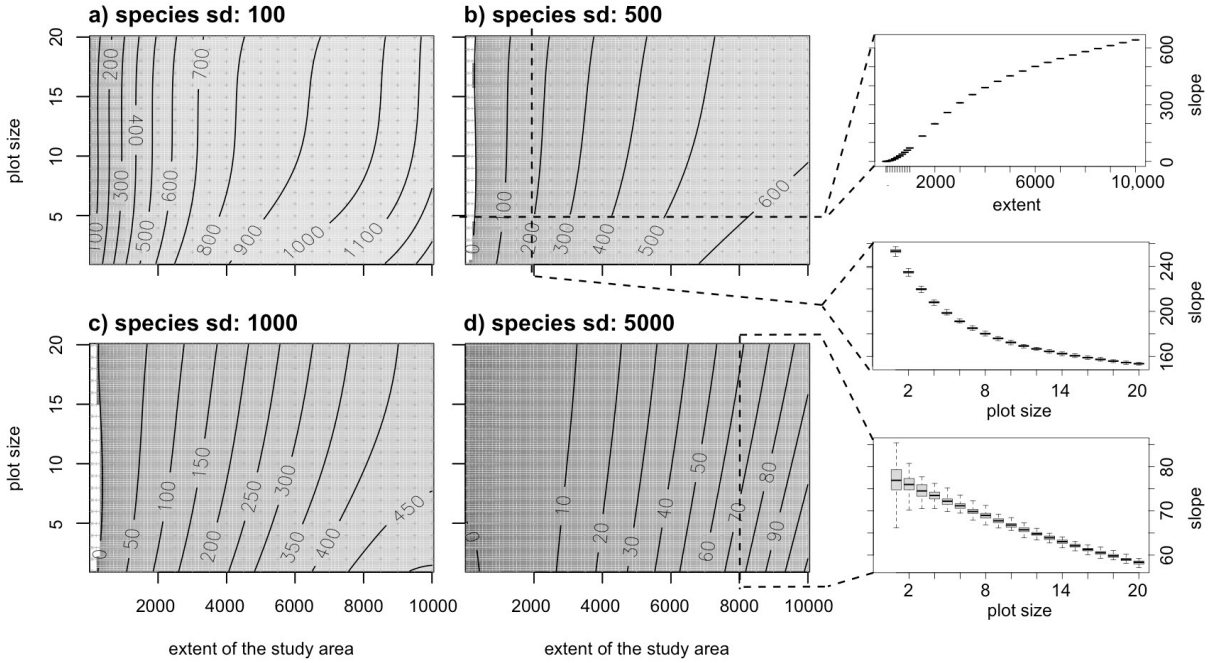

Figure 3: *Variation in slope with a change in plot size and study extent for four different species characteristics (standard deviation 100, 500, 1000 and 5000; Simpson similarity, generalised linear regression with log-link function, with zero similarities and log-transformed distance values). Plot size and slope is measured in artificial units. Slope represents the median of 1000 replicates and was multiplied with -1000 to improve visualisation.*

DISCUSSION

We found that currently used distance-decay relationships are strongly affected by grain size and study extent, rendering direct comparisons of distance-decay relationships across a set of differently designed studies problematic. One might question whether findings in a one-dimensional landscape with evenly spaced and equally abundant species are relevant for a real world application. But, if the distance decay method is not able to capture the clear pattern within this simplified landscape, it is very unlikely (though admittedly not impossible) that the complexity of real world landscapes ameliorates this problem. Pre-analyses with more realistic landscapes (each species with a different abundance and random mean value) indicated comparable dependencies of the distance decay relation on extent and grain size.

Scale dependent ecological and environmental processes were suggested as an explanation for the variation of distance decay results with differences in grain and extent in empirical studies (Soininen *et al.*, 2007; Girdler & Barrie, 2008; Maloney & Munguia, 2011; Martiny *et al.*, 2011; Soininen *et al.*, 2011). However, the results of the here presented simulation study provide strong evidence that the calculation of distance decay relations could strongly be biased by study extent and grain size.

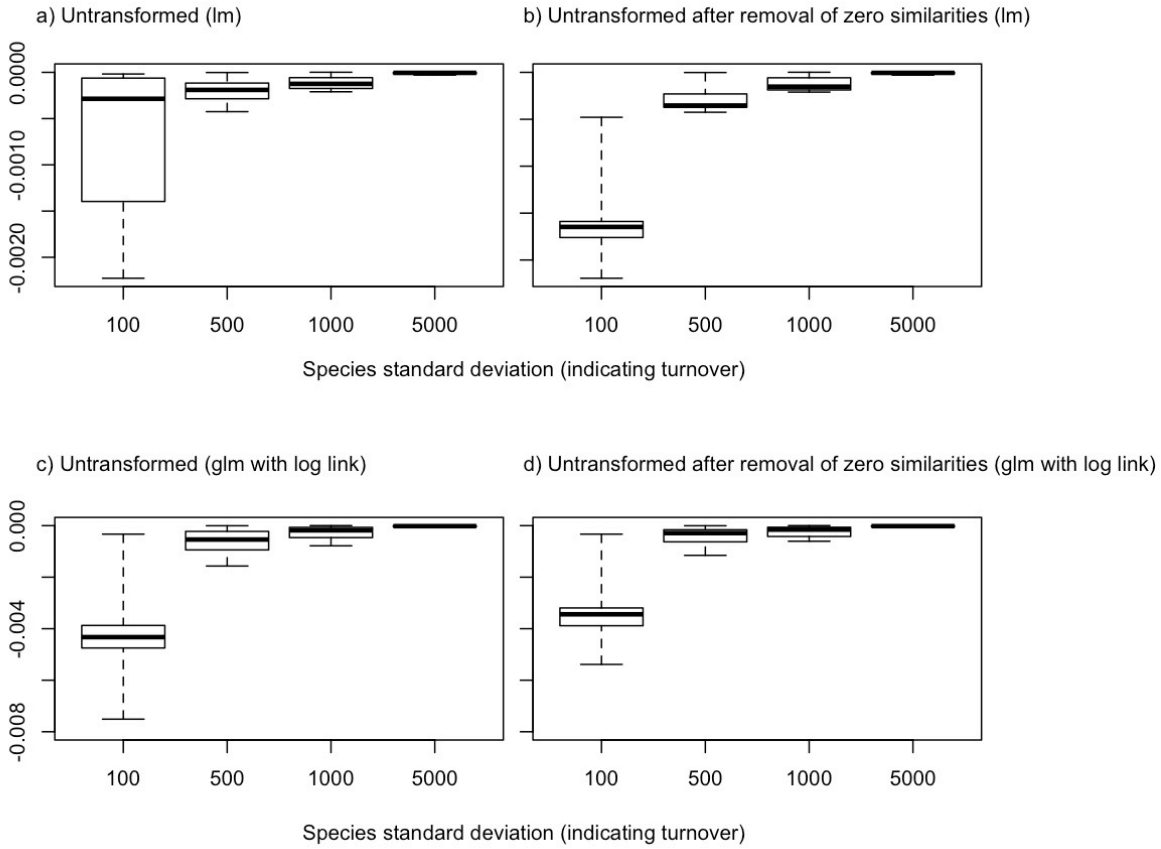

Figure 4: *Currently used distance decay measures (slope of the regression lines, here based on Simpson similarity) performed weakly in detecting the original species standard deviations of the artificial data. Approaches that better cope with zero similarity values (e.g. generalised linear models or removal of zero similarities) show better differentiation. Whiskers extend to the most distant data point; the bold line indicates the median.*

In this study we did not find a simple function relating the dependency of slope on extent and/or grain size to species properties. However, it seems that the better an approach can cope with zero similarity values, the less it is affected by variation in grain size and study extent. Thus removing zero similarities from the data prior to the distance decay analysis increase its power to distinguish between different species standard deviations. However, the approach that currently best copes with changes in grain and extent – albeit it is still not independent – is the application of generalized linear models with a log link function (Millar *et al.* 2011), no matter whether zeros are removed or not. Still currently employed distance decay measures are neither robust nor precise and therefore not a suitable method to identify and assess differences between ecosystems with regard to spatial processes. This is also true for cases were changes in similarity in species composition are investigated along temporal gradients (Korhonen et al., 2010).

In our investigation we found studies with a small spatial extent relative to the species standard deviation not to cover a sufficient portion of the gradient of turnover, resulting in an increase of the slope with spatial extent. Approaches that are less suitable to cope with zero or very small values of similarity (all based on linear model approximations) reached a culmination point of slope after which it was declining again. This flattening of the slope with increasing extent was caused by zero similarities between very distant plots when they were not removed before employing the linear regression. The GLM approach exhibited a contrasting pattern, namely a continuous increase of the slope with increasing study extent. The underlying cause is however again the increasing influence of low similarities at larger distances. While for the untrans-

formed and log(x+1) transformed similarity values a shallower slope is required to fit these points, a steeper slope (i.e. stronger exponential decay) is required when using the log-link.

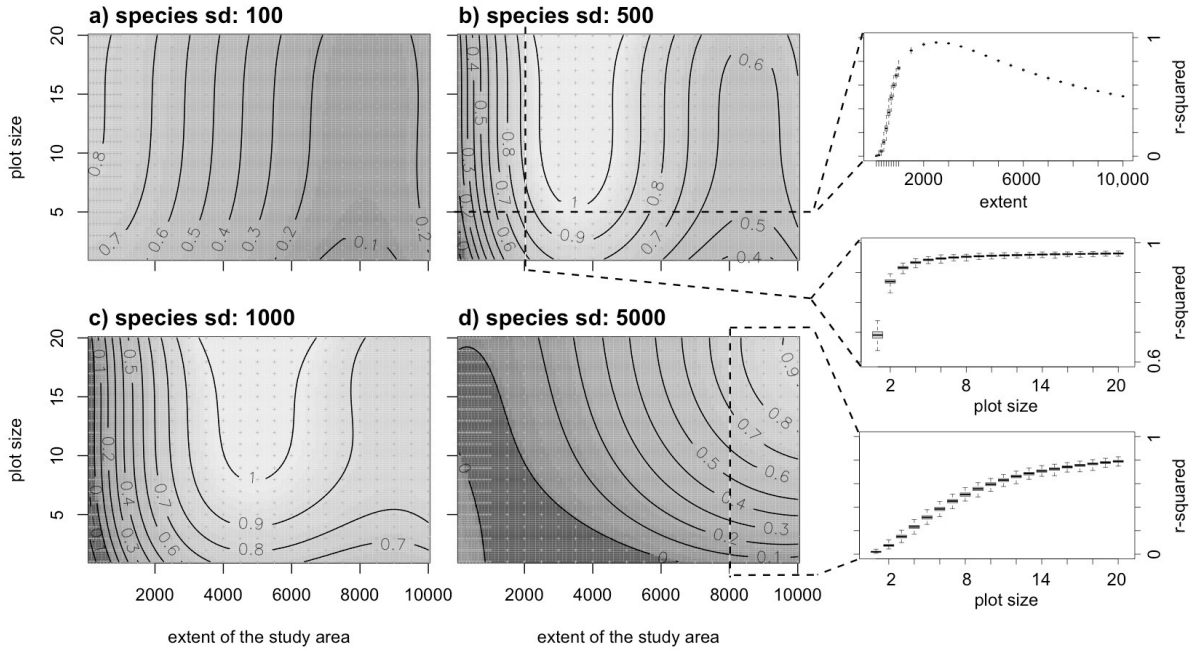

Figure 5: *Variation in goodness of fit indicator r^2 with a change in plot size and study extent for four different species characteristics (standard deviation 100, 500, 1000 and 5000; Simpson similarity, linear regression with zero similarities and untransformed variables). Plot size is measured in artificial units. r^2 represents the median of 1000 iterations.*

The initial increase of slope with plot size is likely due to the high variability in recorded species presences, leading to high dissimilarity even between neighbouring plots and thus low decay in space. As plot sizes get very large, species even far from their optima are included in the sample, leading to high similarity even between distant plots and thus again low decay. The pattern of r^2 is similar to that of slope. The values of r^2 increase initially with study extent because of two factors: for a given slope, r^2 increases as the range of the explanatory variable (here: distances between plots) increases (assuming that the error variance remains unchanged), and the slope itself increases as discussed above. At extents beyond about 4 species' distribution standard deviations r^2 decreases again because the decline in slope outweighs the increased range of the explanatory variable. Finally, r^2 increases monotonously with plot size because sampling error decreases with plot size, too.
Further, similarity indices measuring "differentiation diversity" (sensu Jurasinski *et al.*, 2009) do not treat species equally. Adding another species to two community samples, which share only few species, causes a stronger increase in Simpson and Sørensen similarity than adding a species to samples, which already share most of their species. The same effect occurs if the proportion of shared species is equal but species richness changes.
The results of our simplified simulation study can be compared to empirical studies: Slopes reported for distance decay studies on plants (untransformed) ranged from 0.01 per 100 km (Tuomisto *et al.*, 2003; landscape extent of 1500 km) to 38 per 100 km (Hassler *et al.*, 2010; landscape extent of 0.6 km). Macroecological studies tend to show a less steep decline (shallower slope) and higher goodness of fit (r^2) compared to studies of smaller spatial extent (see table A1 for examples with plant species). Studies of small spatial extent frequently exhibit extraordinarily steep slopes (Hassler *et al.* 2010; Jones *et al*. 2006). In empirical distance decay studies the slope thus declined with increasing extent. Interpreting this with reference to the results of the simulation study suggests that the extents of empirical distance decay studies lie beyond the culmination point being potentially biased by low similarity values of larger dis-

tance comparisons. As the distribution range of many real species is known to be larger than the spatial extent in most studies, this presents an obvious contradiction.

We assume that differences between theoretical expectations from our study and empirical observations are due to clumped occurrences of individuals of the same species (Morlon *et al.* 2008) in real landscapes. This aggregated occurrence of individuals of one species may effectively mimic a smaller distribution range of the species when the distance between the populations is relatively large. A further explanation resolving the contradiction between simulated and real data refers to the occurrence and distribution of rare species. Typically, abundance and frequency distributions of species are extremely right-skewed, resulting in many rare species (Gaston & Blackburn 2000). These uneven quantitative species properties potentially influence the real world distance decay relation. Hubbell (2001) suggests that an initial steep decline in community similarity with distance is induced by the small-scale occurrence of rare species, while common and widespread species are responsible for the following shallower decay. In contrast to this, empirical studies are indicating that the removal of rare species has negligible effects on the distance decay relation (Nekola & White, 1999; Morlon *et al.*, 2008; Heino & Soininen, 2010).

Another reason for the steep slopes of studies of very small extent is of statistical nature: A higher sample size is needed in order to detect shallow slopes with significant p-values compared to steep slopes, assuming that the variance of the error and the range of the explanatory variable is the same in both cases. Thus, a steeper slope is more easily tested to be significant with a given number of records than a shallow one. In empirical studies aiming to detect shallow slopes the sampling effort is high. Especially for tropical forests, Jones *et al.* (2006) highlighted a decreasing goodness of fit (r^2) with decreasing study area extent. This is also supported by the comparison of studies in table A1. Non-significant relations are usually not published and thus not reported to the scientific community resulting in the so called "publication bias" (Jennions & Møller 2002).

The impact of more realistic spatial patterns in species distributions on distance decay relations, like unequally spaced distributions of their centres, varying ranges, clumping of individuals of the same species as well as the occurrence of rare species is not yet fully identified. However, methodological restrictions would apply even if these factors were considered. Regardless of these open questions, we recommend that distance decay studies differing in grain and extent should not be directly compared due to complex dependencies and lacking robustness of the currently used distance decay measures.

The central idea of distance-decay analyses is the measurement of change in community structure along a spatial, temporal or environmental gradient, which is suggested to represent a crucial part of beta diversity (Anderson et al. 2011). Since these spatial patterns in the distribution of biota are of increasing interest, especially in the face of regional biodiversity loss, more robust methods, that are less dependent on sampling design, need to be developed for this relevant field of research. While the here tested common methods are not robust enough this does not exclude the possibility of more robust methods being developed. The application of generalised linear models with a log link function appears to be a first step in the right direction.

REFERENCES

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C. & Swenson, N.G. (2011) Navigating the multiple meanings of b diversity: a roadmap for the practicing ecologist. *Ecology Letters,* **14**,19–28.

Arrhenius, O. (1921) Species and area. *Journal of Ecology*, **9**, 95–99.

Astorga, A., Oksanen, J., Luoto, M., Soininen, J., Virtanen, R. & Muotka, T. (2011) Distance decay of similarity in freshwater communities: do macro- and microorganisms follow the same rules? *Global Ecology and Biogeography*, Article first published online: 14 June 2011; doi: 10.1111/j.1466-8238.2011.00681.x

Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, **19**, 134–143.

Beierkuhnlein, C. (1998) Biodiversität und Raum. *Die Erde*, **128**, 81–101.

Chave, J. & Leigh, E.G. (2002) A spatially explicit neutral model of beta-diversity in tropical forests. *Theoretical Population Biology*, **62**, 153–168.

Condit, R., Pitman, N., Leigh, E.G., Chave, J., Terborgh, J., Foster, R.B., Nunez, P., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H.C., Losos, E. & Hubbell, S.P. (2002) Beta-diversity in tropical forest trees. *Science*, **295**, 666–669.

Dengler, J., Löbel, S. & Dolnik, C. (2009) Species constancy depends on plot size - a problem for vegetation classification and how it can be solved. *Journal of Vegetation Science*, **20**, 754–766.

Dice, L.R. (1945) Measures of the amount of ecological asso- ciation between species. *Ecology*, **26**, 297–302.

Duivenvoorden, J.F., Svenning, J.C. & Wright, S.J. (2002) Beta-diversity in tropical forests - response. *Science*, **297**, 636.

Duque, Á., Phillips, J.F., von Hildebrand, P., Posada, C.A., Prieto, A., Rudas, A., Suescún, M. & Stevenson, P. (2009) Distance decay of tree species similarity in protected areas on terra firme forests in Colombian Amazonia. *Biotropica*, **41**, 599–607.

Fattorini, S. (2010) The influence of geographical and ecological factors on island beta diversity patterns. *Journal of Biogeography*, **37**, 1061–1070.

Garcillán, P.P. & Ezcurra, E. (2003) Biogeographic regions and beta-diversity of woody dryland legumes in the Baja California peninsula. *Journal of Vegetation Science*, **14**, 859–868.

Gaston, K.J. & Blackburn, T.M. (2000). Pattern and Process in Macroecology, Blackwell Science, Oxford.

Girdler, E.B. & Barrie, B.T.C. (2008) The scale-dependent importance of habitat factors and dispersal limitation in structuring Great Lakes shoreline plant communities. *Plant Ecology*, **198**, 211–223.

Green, J.L., Holmes, A.J., Westoby, M., Oliver, I., Briscoe, D., Dangerfield, M., Gillings, M. & Beattle, A.J. (2004) Spatial scaling of microbial eukaryote diversity. *Nature*, **432**, 747–750.

Hassler, S.K., Kreyling, J., Beierkuhnlein, C., Eisold, J., Samimi, C., Wagenseil, H. & Jentsch, A. (2010) Vegetation pattern divergence between dry and wet season in a semiarid savanna - spatio-temporal dynamics of plant diversity in northwest Namibia. *Journal of Arid Environments*, **74**, 1516-1524 .

Heino, J. & Soininen, J. (2010) Are common species sufficient in describing turnover in aquatic metacommunities along environmental and spatial gradients? *Limnology and Oceanography*, **55**, 2397-2402.

Hubbell, S.P. (2001) The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton.

Jennions, M.D. & Møller, A.P. (2002) Publication bias in ecology and evolution: an empirical assessment using the 'trim and fill' method. *Biological Reviews*, **77**, 211–222.

Jones, M.M., Tuomisto, H., Clark, D.B. & Olivas, P. (2006) Effects of mesoscale environmental heterogeneity and dispersal limitation on floristic variation in rain forest ferns. *Journal of Ecology*, **94**, 181–195.

Jurasinski, G. (2007) simba: A Collection of functions for similarity calculation of binary data. *R package version 0.2-5*.

Jurasinski, G., Retzer, V. & Beierkuhnlein, C. (2009) Inventory, differentiation, and proportional diversity: a consistent terminology for quantifying species diversity. *Oecologia*, **159**, 15–26.

Kallimanis, A.S., Halley, J.M., Vokou, D. & Sgardelis, S.P. (2008) The scale of analysis determines the spatial pattern of woody species diversity in the Mediterranean environment. *Plant Ecology*, **196**, 143–151.

Korhonen, J.J., Soininen, J. & Hillebrand, H. (2010) A quantitative analysis of temporal turnover in aquatic species assemblages across ecosystems. *Ecology*, **91**, 508–517.

Krasnov, B.R., Mouillot, D., Shenbrot, G.I., Khokhlova, I.S., Poulin, R. (2010) Deconstructing spatial patterns in species composition of ectoparasite communities: the relative contribution of host composition, environmental variables and geography. *Global Ecology and Biogeography*, **19**, 515–526.

Kreyling, J., Jentsch, A., Beierkuhnlein, C. (2011) Stochastic trajectories of succession initiated by extreme climatic events. *Ecology Letters*, **14**, 758-764.

La Sorte, F.A., McKinney, M.L., Pyšek, P., Klotz, S., Rapson, G.L., Celesti-Grapow, L. & Thompson, K. (2008) Distance decay of similarity among European urban floras: the impact of anthropogenic activities on beta-diversity. *Global Ecology and Biogeography*, **17**, 363–371.

Lennon, J.J., Koleff, P., Greenwood, J.J.D. & Gaston, K.J. (2001) The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology*, **70**, 966–979.

Lenoir, J., Gegout, J.C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N.E., Dullinger, S., Pauli, H., Willner, W., Grytnes, J.A., Virtanen, R.J. & Svenning, J.C. (2010) Cross-scale analysis of the region effect on vascular plant species diversity in southern and northern European mountain ranges. *PLoS ONE*, **5**, 1-13.

Leeuwen, C.G. van (1970) Raum-zeitliche Beziehungen in der Vegetation. *Gesellschaftsmorphologie (Strukturforschung)* (ed. by R. Tüxen), pp. 63–68. W. Junk, Den Haag.

Lira-Noriega, A., Soberon, J., Navarro-Siguenza, A.G., Nakazawa, Y. & Townsend Peterson, A. (2007) Scale dependency of diversity components estimated from primary biodiversity data and distribution maps. *Diversity and Distribution*, **13**, 185–195.

Maloney, K.O. & Munguia, P. (2011) Distance decay of similarity in temperate aquatic communities: effects of environmental transition zones, distance measure, and life histories. Ecography, **34**, 287-295.

Martiny, J.B., Eisen, J.A., Penn, K., Allison, S.D. & Horner-Devine, M.C. (2011) Drivers of bacterial β-diversity depend on spatial scale. *Proceedings of the National Academy of Sciences*, **108**, 7850-7854.

McKinney, M.L. (2004) Measuring floristic homogenization by non-native plants in North America. *Global Ecology and Biogeography*, **13**, 47-53.

Millar, R.B., Anderson, M.J. & Tolimieri, N. (2011) Much ado about nothings: using zero similarity points in distance-decay curves. *Ecology*, **92**, 1717–1722.

Morlon, H., Chuyong, G., Condit, R., Hubbell, S., Kenfack, D., Thomas, D., Valencia, R. & Green, J.L. (2008) A general framework for the distance decay of similarity in ecological communities. *Ecology Letters*, **11**, 904–917.
Nakamura, K., Suwa, R., Denda, T. & Yokota, M. (2009) Geohistorical and current environmental influences on floristic differentiation in the Ryukyu Archipelago, Japan. *Journal of Biogeography*, **36**, 919–928.
Nekola, J.C. & Brown, J.H. (2007) The wealth of species: ecological communities, complex systems and the legacy of Frank Preston. *Ecology Letters*, **10**, 188–196.
Nekola, J.C. & White, P.S. (1999) The distance decay of similarity in biogeography and ecology. *Journal of Biogeography*, **26**, 867–878.
Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., O'Hara, R.G., Simpson, G.L., Solymos, P., Stevens, M.H. & Wagner, H. (2010) vegan: Community Ecology Package, R package version 1.17-0.
Palmer, M.W. & White, P.S. (1994) Scale dependence and the species-area relationship. *American Naturalist*, **144**, 717–740.
Preston, F.W. (1962) Canonical distribution of commonness and rarity: Part 2. *Ecology*, **43**, 410–432.
Qian, H. (2008) A latitudinal gradient of beta diversity for exotic vascular plant species in North America. *Diversity and Distribution*, **14**, 556–560.
Qian, H., Ricklefs, R.E. & White, P.S. (2005) Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. *Ecology Letters*, **8**, 15–22.
Qian, H., Badgley, C. & Fox, D.L. (2009) The latitudinal gradient of beta diversity in relation to climate and topography for mammals in North America. *Global Ecology and Biogeography*, **18**, 111–122.
Qian, H. (2009) Beta diversity in relation to dispersal ability for vascular plants in North America. *Global Ecology and Biogeography*, **18**, 327–332.
R Development Core Team (2010) R: A Language and Environment for Statistical Computing, Vienna.
Ruokolainen, K. & Tuomisto, H. (2002) Beta diversity in tropical forests - Response. *Science*, **297**, 1439.
Simpson, G.G. (1943) Mammals and the nature of continents. *American Journal of Science*, **241**, 1–31.
Soininen, J., McDonald, R. & Hillebrand, H. (2007) The distance decay of similarity in ecological communities. *Ecography*, **30**, 3–12.
Soininen, J. (2010) Species Turnover along Abiotic and Biotic Gradients: Patterns in Space Equal Patterns in Time? *BioScience*, **60**, 433-439.
Soininen, J., Korhonen, J.J., Karhu, J. & Vetterli, A. (2011) Disentangling the spatial patterns in community composition of prokaryotic and eukaryotic lake plankton. *Limnology & Oceanography,* **56**, 508-520.
Sørensen, T.A. (1948) A method of establishing groups of equal amplitude in plant sociology based on similarity of species content, and its application to analyses of the vegetation on Danish commons. *Kongelige Danske Videnskabernes Selskabs Biologiske Skrifter*, **5**, 1–34.
Steinbauer, M.J. & Beierkuhnlein, C. (2010) Characteristic pattern of species diversity on the Canary Islands. *Erdkunde*, **64**, 57–71.
Steinitz, O., Heller, J., Tsoar, A., Rotem, D. & Kadmon, R. (2005) Predicting regional patterns of similarity in species composition for conservation planning. *Conservation Biology*, **19**, 1978–1988.
Tuomisto, H., Ruokolainen, K. & Yli-Halla, M. (2003) Dispersal, environment, and floristic variation of western Amazonian forests. *Science*, **299**, 241–244.
Uddin, M.B., Steinbauer, M.J., & Beierkuhnlein, C. (2011) Stand characteristics and spatial species aggregation in a Bangladesh forest ecosystem. *Diversity*, **3**, 453-465.
Whittaker, R.H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, **30**, 280–338.
Whittaker, R.H. (1972) Evolution and measurement of species diversity. *Taxon*, 21, 213–251.
Williams, M.R., Lamot, B.B. & Henstridge, J.D. (2009) Species–area functions revisited. *Journal of Biogeography*, **36**, 1994-2004.
Winter, M., Kühn, I., La Sorte, F.A., Schweiger, O., Nentwig, W. & Klotz, S. (2010) The role of non-native plants and vertebrates in defining patterns of compositional dissimilarity within and across continents. *Global Ecology and Biogeography*, **19**, 332–342.
Wilson, J.B. (2007) Priorities in statistics, the sensitive feet of elephants, and don't transform data. *Folia Geobotanica*, 42, 161–167.
Zurell, D., Berger, U., Cabral, J.S., Jeltsch, F., Meynard, C.N., Münkemüller, T., Nehrbass, N., Pagel, J., Reineking, B., Schröder, B. & Grimm, V. (2010) The virtual ecologist approach: simulating data and observers. *Oikos*, **119**, 622-635.

BIOSKETCHES

Manuel J. Steinbauer has research interests in the fields of biogeography, macroecology, global change ecology, spatial ecology and numerical and statistical ecology. Particular interests include the role of scale in ecology with special focus on islands.

Klara Dolos works in the field of forest landscape modelling. She is especially interested in the consequences of interactions between forest disturbances and examines factors influencing the stability of temperate forests, particularly with regard to climate change.

Björn Reineking is head of the group on Biogeographical modelling. He is interested in the mechanisms that determine the distribution and abundance of organisms at various spatial scales. His particular focus lies on the interplay of species traits, dynamic processes like dispersal, and environmental conditions.
Carl Beierkuhnlein is head of the department of Biogeography at the University of Bayreuth. His working group is especially focussing on biodiversity assessments, island biogeography, experimental ecology, and climate change ecology. He is especially interested in the understanding of ecosystem form and functioning at varying spatial and temporal scales.

Supplementary Material

Additional Supporting Information may be found in the online version of this article:
Appendix S1 {Figures with additional findings and illustrations}
Appendix S2 {Extent, grain, slope and r^2 of empirical distance decay studies on plants}
Appendix S3 {R-code for simulations}

APPENDIX S1:

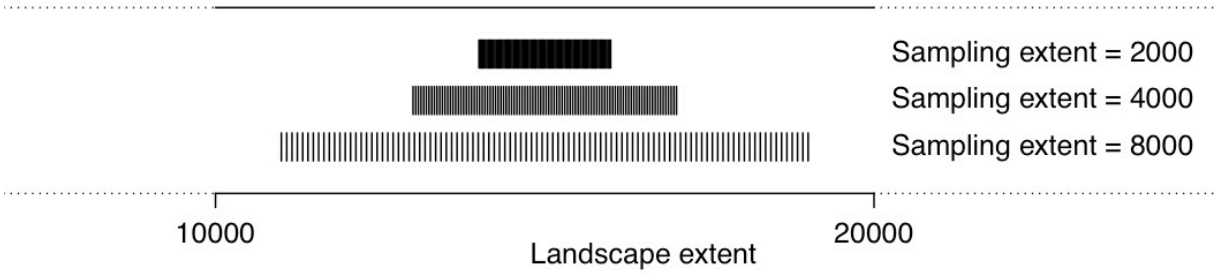

Figure A1: *Within the central 10,000 landscape units (10,001-20,000) the study extent was randomly placed and 100 even sized equidistant survey plots sampled.*

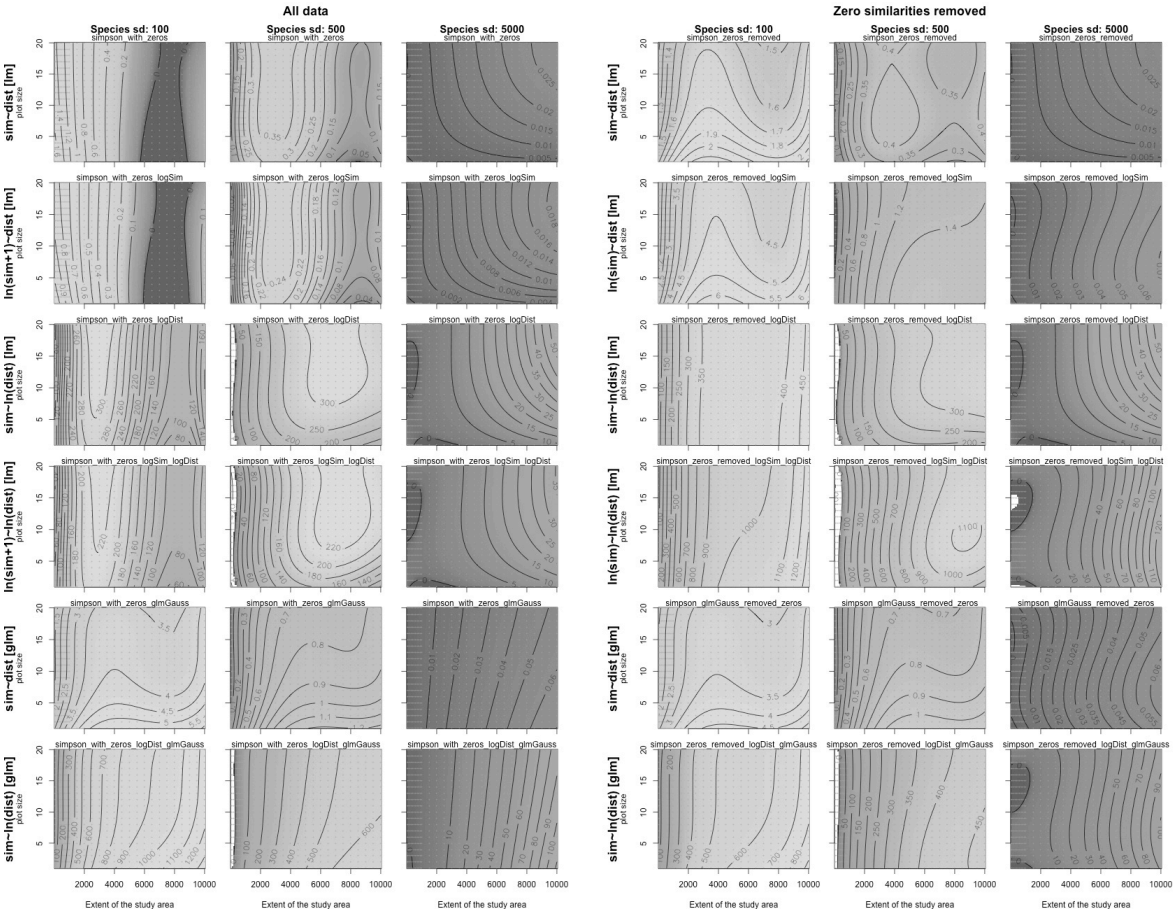

Figure A2: *Simpson similarity and the influence of different transformations of similarity and/or distance on the slope of the distance-decay relationship. Slope represents the median of 1000 replicates and was multiplied with -1000 to improve visualisation.*

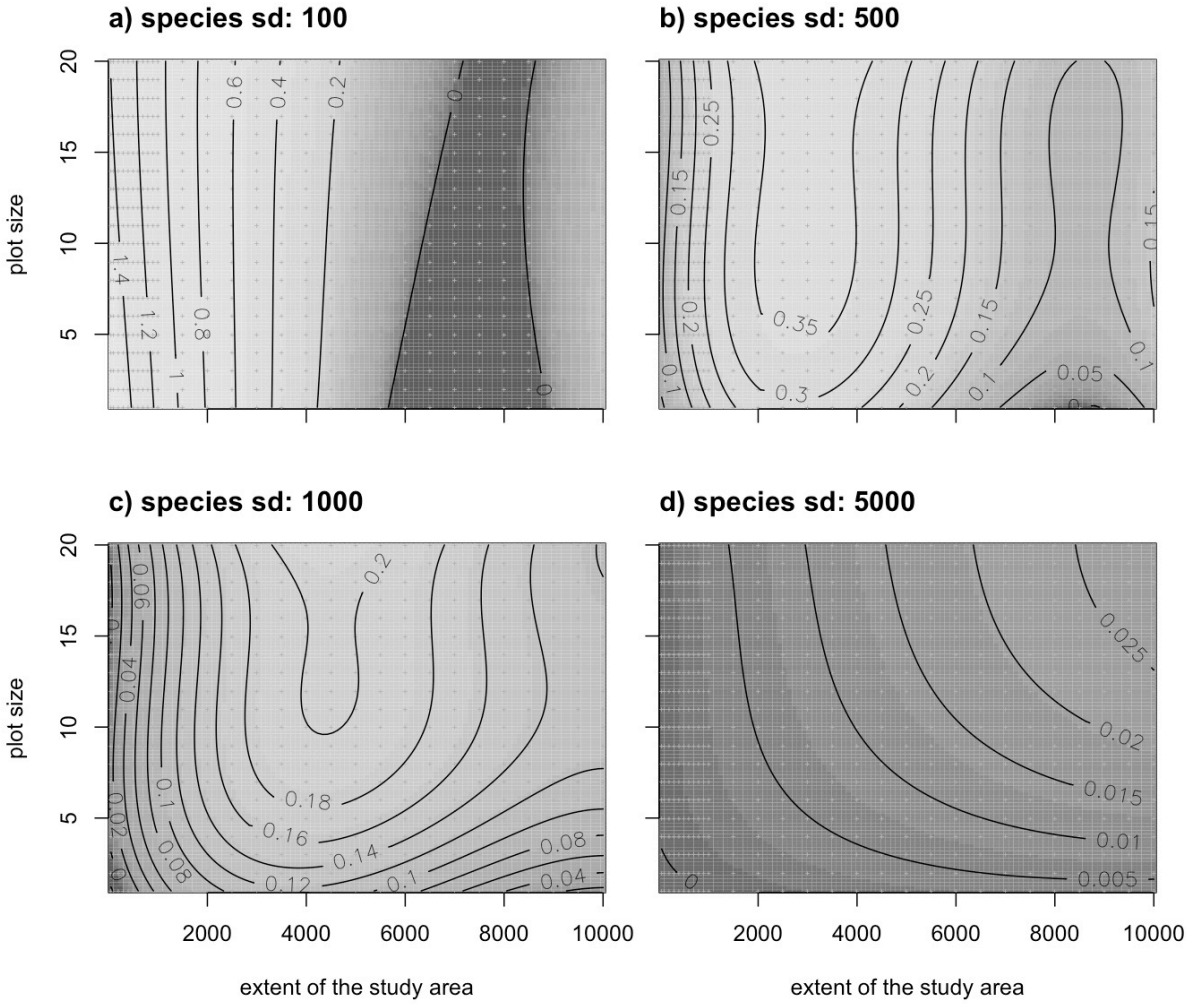

Figure A3: *Variation in slope of the distance-decay relationship with a change in plot size and study extent for four different species characteristics (standard deviation 100, 500, 1000 and 5000; same as figure 2 but for Sørensen similarity). Plot size and slope is measured in artificial units. Slope represents the median of 1000 replicates and was multiplied with -1000 to improve visualisation.*

APPENDIX S2:

Table A1: *Slope and goodness of fit for different studies on plant species all calculating distance decay relation with a norm-norm model.*
**recalculated with Jaccard similarity to enable a comparison*
#slope was estimated from the published figure

slope per 100 km	r^2	extent (km)	plot size (m^2)	similarity metric	biota	system studied	location	source
0. 019	**?**	2000 km	?	Simpson	urban floras	urban areas	Europe	LaSorte et al. (2008)
0.012 #	0.26	1500 km	2500	Jaccard	melastomes	terra firma forest/ Melastomataceae	South America	Tuomisto et al. (2003)
0.011 #	0.17	1500 km	2500	Jaccard	pteridophytes	terra firma forest/ pteridophytes	South America	Tuomisto et al. (2003)
0.013	0.07	1043 km	$1*10^6$ - $1206*10^6$	Jaccard	vascular plants	oceanic islands	Japan	Nakamura et al. (2009)*
0.058	0.61	400 km	$269*10^6$ - $2034*10^6$	Jaccard	vascular plants	oceanic islands	Canary Islands	Steinbauer & Beierkuhnlein (2010) *
0.043 #	0.68	170 km	2500	Sørensen	palm flora	terra firma forest	South America	Vormisto et al. (2004)
18 - 43	0.02 - 0.25	0.3 - 1 km	0.24	Jaccard	plant species	shoreline	Lake Michigan	Girdler and Barrie (2008)
17 - 65	0.03 - 0.04	0.6 km	81.5	Jaccard	plant species	African savannas	northwest Namibia	Hassler et al. (2010) *

APPENDIX S3:

R-CODE

```
#############################################################
### LIBRARIES
library(simba)

### FUNCTIONS
sample.species.presence <- function(species.sd, plot.width=1, sample.extent=1500, n.species=100,
world.extent=30000, species.density = 1000, n.sample.sites = 100) {
   # Create the landscape, e.g. the date on which the distance decay measures are
   # applied.
   # Arguments
      # species.sd: Standard deviation of the normally distributed species. The higher
      # species.sd the wider is the range of the species.
      # plot.width: Size of the sampled area.
      # sample.extent: Length of the region where sampling plots are placed.
      # n.species: Number of species placed within the landscape.
      # world.extent: Size of the landscape
      # species.density: Abundance of species in the landscape.
      # n.sample.sites: Number equidistant survey plots within sample.extent.
   # Value
      # List with two elements. First element constitutes the vegetation data,
      # second element contains the sampling positions.

  species.mu <- seq(1, world.extent, len=n.species)
  start.location <- world.extent/3
  locations <- seq(from=start.location, to=start.location + sample.extent, len=n.sample.sites)

  p <- sapply(locations, function(x) pnorm(x + 1/2, species.mu, species.sd) - pnorm(x - 1/2,
  species.mu, species.sd))
  p.obs <- 1 - dbinom(0, size=species.density * plot.width, prob=p)
  list(vegdata = matrix(rbinom(n.species*n.sample.sites, 1, prob=p.obs), nrow=nrow(p.obs)),
  locations=locations)
}


calculate.distance.decay <- function(data, index.function = function(x) 1 - sim(x, method="simpson"), const = 1) {
   # Calculate distance decay measures for a given data set using different
   # transformations and regressions.
   # Arguments
      # data: Result of function sample.species.presence().
         # index.function: Function to calculate the similarity index.
      # const: Constant to be added for cases where the similarity index is
         # log-transformed and the data contain zero similarities.
   # Value
      # Data frame with results of the distance decay calculations.


   extract.model.stats <- function(model) {c("slope" = unname(coef(model)[2]), "r.squared" = 1 –
   model$deviance / model$null.deviance) }

   distance <- c(dist(data$locations))
   index <- index.function(t(data$vegdata))
   full.data <- data.frame(cbind(index, distance))
   nozero.data <- subset(full.data, is.finite(log(index)))

   settings <- expand.grid("y" = c("index", "log(index)", "log(index + const)"),
                           "x" = c("distance", "log(distance)"),
                           "data" = c("full.data", "nozero.data"),
                           "link" = c("log", "identity"))
   settings <- subset(settings, !(y == "log(index)" & data != "nozero.data"))
   settings <- subset(settings, !(y == "log(index + const)" & data == "nozero.data"))
```

```
  settings <- subset(settings, !(link == "log" & y != "index"))
  rownames(settings) <- NULL
  res <- t(apply(settings, 1,
          function(set) {
                  extract.model.stats(eval(parse(text = paste("glm(",  set[["y"]], " ~ ", set[["x"]], ", data
  = ", set[["data"]], ", family = gaussian(link = ", set[["link"]], "), start=c(0,0))", sep=""))))}))
  cbind(settings, res)
}

simulate.distance.decay <- function(species.sd.vector=c(200, 500), plot.width.vector=c(1,5), sam-
ple.extent.vector=c(500, 1000), index.functions = list("simpson" = function(x) 1 - sim(x, method="simpson"), "soeren-
sen" = function(x) sim(x, method="soerensen") ), n.species=1000, world.extent=30000, species.density = 1000,
n.sample.sites = 100, niter=100, const=1, verbose = TRUE) {
  # Iterate the distance decay analysis. The functions sample.species.presence and
  # calculate.distance.decay are called.
  # Arguments
      # species.sd: Standart deviation of the normally distributed species. The higher
      # species.sd the wider is the range of the species.
      # plot.width: Size of the sampled area.
      # sample.extent: Length of the region where sampling plots are placed.
      # n.species: Number of species placed within the landscape.
      # world.extent: Size of the landscape
      # species.density: Abundance of species in the landscape.
      # n.sample.sites: Number equidistant survey plots within sample.extent
      # niter: Number of replicates for each parameter combination.
      # index.function: Function to calculate the similarity index.
      # const: Constant to be added for cases where the similarity index is
      # log-tranfsormed and the data contain zero similarities.
      # verbose: Logical indicator if progress information of the simulation should
      # be given or not.
  # Value
      # Data frame containing the simulation results with columns
      # y: Transformation of the response variable (index).
      # x: Transformation of the explanatory variable (distance).
      # data: Data set information. Data contained zero similarities or not.
      # link: Link function.
      # slope: Slope of the regression line.
      # r.squared: Adjusted r-squared of the linear regressions.
      # species.sd: Species standart deviation used for the simulation.
      # plot.width: Plot size used for the simulation.
      # sample.extent: Sample extent used for the simulation.
      # index: Name of the calculated similarity index.
      # replicate: ID of the replicate, e.g. of the simulated data set.
      # nr: ID of parameter combinations (species.sd, plot.width, sample.extent).

  parameter.combinations <- expand.grid(species.sd = species.sd.vector, plot.width =
  plot.width.vector, sample.extent = sample.extent.vector, index = names(index.functions), replicate
  = 1:niter)
  parameter.combinations$nr <- 1:nrow(parameter.combinations)

  if (verbose) cat("Number of simulations: ", nrow(parameter.combinations), "\n")

  result <- apply(parameter.combinations, 1, function(x) {
                      if (verbose) {
                    nr <- as.numeric(x[["nr"]])
                    if (nr %% 50  == 0) cat("\n")
                    cat(nr, " ")
                  }

  data <- sample.species.presence(species.sd = as.numeric(x[["species.sd"]]), plot.width =
  as.numeric(x[["plot.width"]]), sample.extent = as.numeric(x[["sample.extent"]]), n.species =
  n.species, world.extent = world.extent, species.density = species.density, n.sample.sites =
  n.sample.sites)

  try(calculate.distance.decay(data, index.function = index.functions[[x[["index"]]]], const =
```

```
                const))
  })

  for (i in seq(result)) {
          if (!inherits(result[[i]], "try-error")) {
                  result[[i]] <- cbind(result[[i]], parameter.combinations[rep(i, NROW(result[[i]])),])
          } else {
                  result[[i]] <- cbind(data.frame(y = NA, x = NA, data = NA, link = NA, slope = NA,
                  r.squared = NA), parameter.combinations[i,])
          }}
  do.call(rbind, result)
}

### EXAMPLE
species.sd.vector <- c(100, 500, 1000, 5000)
plot.width.vector <- 1:20
sample.extent.vector <- c(50, 100, 200, 300, 400, 500, 600, 700, 800, 900, 1000, 1500, 2000, 2500, 3000, 3500,
4000, 4500, 5000, 5500, 6000, 6500, 7000, 7500, 8000, 8500, 9000, 9500, 10000)
world.extent <- 30000
n.species <- 1000
niter <- 100

result <- simulate.distance.decay(species.sd.vector = species.sd.vector, plot.width.vector = plot.width.vector, sam-
ple.extent.vector = sample.extent.vector, index.functions = list("simpson" = function(x) 1 - sim(x, method = "simp-
son"), "soerensen" = function(x) sim(x, method = "soerensen") ), n.species = 1000, world.extent = 30000, spe-
cies.density = 1000, n.sample.sites = 100, niter = niter, const = 1, verbose = TRUE)
```

3. Manuscript 2 - Increase of island endemism with altitude – speciation processes on oceanic islands.

Ecography 35 (2012) DOI: 10.1111/j.1600-0587.2011.07064.x

Manuel Jonas Steinbauer, Rüdiger Otto, Agustín Naranjo-Cigala, Carl Beierkuhnlein, José-María Fernández-Palacios

M.J. Steinbauer (Manuel.Steinbauer@uni-bayreuth.de) and C. Beierkuhnlein, Lehrstuhl Biogeografie, Universität Bayreuth, D-95447 Bayreuth, Germany
R. Otto and J.M. Fernández-Palacios, Departmento de Ecología, Facultad de Biología, Universidad de La Laguna, ES-38206 La Laguna, Tenerife, Islas Canarias, Spain
A. N. Cigala, Departamento de Geografía, Universidad de Las Palmas de Gran Canaria, 35003, Las Palmas de Gran Canaria, Islas Canarias, Spain

Abstract
Understanding speciation on oceanic islands is a major topic in current research on island biogeography. Within this context, it is not an easy task to differentiate between the influence of elevation as an indicator for habitat diversity and island age as an indicator for the time available for diversification. One reason for this is that erosion processes reduce the elevation of islands over time. In addition, the geographic distance to source ecosystems might differ among habitats, which could lead to habitat-specific reduction of species immigration, niche occupation and diversification. We used the percentage of single island endemic species (pSIE) in five different zonal ecosystems (distributed in altitude) on the Canary Islands as an indicator for diversification. We tested whether diversification increases with altitude due to a greater ecological isolation of high elevation ecosystems on oceanic islands under the assumption of a low elevation source region on the mainland. In addition we tested whether the "hump-shaped" (unimodal) relationship between pSIE and island age as well as the linear relationship between species richness and pSIE is consistent across spatial scales. We also analyse a potential influence of island area and habitat area. We found that pSIE increases with elevation. The relations between species richness as well as age with pSIE are consistent across scales. We conclude that high elevation ecosystems are ecologically isolated. Surprisingly, the altitudinal belt with the strongest human influences has the highest values of pSIE. We successfully transfer the "general dynamic theory of island biogeography" to the ecosystem scale, which provides multiple opportunities for future studies. With this approach we find that the effects of elevation on diversification can be separated from those of island age.

Introduction

Species distribution on island archipelagos depends on immigration, extinction and speciation. Separating the effects and interactions of these processes is not an easy task. Recently, the importance of diversification on islands has been particularly emphasised. Emerson and Kolm (2005a) suggest using the percentage of single-island endemics (pSIE) as an indicator for diversification on island archipelagos. Working with data on arthropods and seed plants for both the Canary and Hawaii Islands they found pSIE to be strongly correlated with species richness. They propose that species richness promotes speciation due to intensified interspecific competition leading to extinction and genetic adaptation. This "diversity-driven speciation" hypothesis has been discussed by various authors (Cadena et al. 2005, Kiflawi et al. 2007, Pereira et al. 2007, Whittaker et al. 2007, Witt and Maliakal-Witt 2007, Gruner et al. 2008, Birand and Howard 2008, Vilenkin et al. 2009). Cadena et al. (2005) argue that both species richness as well as endemism is influenced by island age leading to a fortuitous correlation of the variables. This is the case, as on the one hand endemic species will accumulate on an island over time and local populations differentiate while populations on other islands become extinct. On the other hand the species number will always increase with island age through colonisation as long as extinction rates are relatively low. However, the latter statement is only valid for islands where equilibrium has not been reached (Emerson and Kolm 2005b).

In their "island immaturity speciation pulse model" Whittaker et al. (2007) suggested island age as a key parameter determining species distribution and endemism. They postulated a concept of island evolution that starts with an early island stage in which an island reaches maximum area and altitude through volcanic activity over an erosion-driven topographically and geologically heterogeneous development to a flat, topographically simple island that ultimately disappears beneath the sea's surface. In their theoretical model, speciation is driven by the availability of non-occupied ecological niches and is highest at a stage in the island's development with time when the species number has not yet reached its carrying capacity. The model was further refined by Whittaker et al. (2008, 2010). According to the model of Whittaker et al. (2007, 2008, 2010), pSIE follows an idealised hump-shaped curve following the ontogeny of an island: At the beginning, when species are immigrating from nearby islands, no SIE will be present on the newly formed island. Due to the limited number of species, the availability of ecological niches is high and the speciation rate (and simultaneously pSIE) will also increase. With the island becoming older a development stage is reached whereby more species will become extinct than those newly established on the island (either due to speciation or immigration). According to Whittaker et al. (2008) not only the species number and the number of SIE but also the pSIE will decline. Several reasons are mentioned: Firstly, SIE may colonise newly established islands within the archipelago and thus lose their status as SIE. Secondly, it is said that multi-island endemics and non-endemic species are viable in smaller population sizes due to a possible immigration from other islands (Triantis et al. 2008). Thus, SIE are more likely to go extinct with the decline in suitable habitat due to a decline in island area. Thirdly, an increase in habitat similarity within the island and with neighbouring islands due to a flattening of the island will result in a decrease in speciation of neo-endemic habitat specialists, while coastal generalists will persist. In general this assumption would also predict low pSIE for coastal ecosystems.

Several authors have discussed whether or not null models could describe the investigated link between pSIE and species richness for both the Canary Islands (Kiflawi et al. 2007, Witt and Maliakal-Witt 2007, Emerson and Kolm 2007, Birand and Howard 2008) and Hawaii (Gruner et al. 2008). The question is whether the apparent positive correlation between total species number and the percentage of endemics is coincidental or not. Vilenkin et al. (2009) argue that the observed patterns might be the by-product of an exponential relationship between the numbers of co-occurring endemic and non-endemic species caused by narrower ranges of endemic species compared to co-occurring non-endemic species. Pereira et al. (2007) pointed out that species richness and pSIE are correlated with various physical variables such as island size and elevation. It is therefore likely that the correlation between species richness and pSIE reflects a

dependency on different variables or, more likely, on the same variable but through different mechanisms that have not yet been detected.
In this paper we suggest mechanisms that could describe the correlation of species richness and pSIE based on general island biogeography processes. We test the hypothesis that species distribution depends on the availability of niche space with speciation being additionally driven by isolation and that both the availability of niche space and isolation are, for the Canary Islands, dependent on elevation (Hypothesis 1). In addition we investigate whether patterns for pSIE and species richness are consistent across scales and therefore could be identified when comparing ecosystems of these islands instead of complete islands (Hypothesis 2).

Theory of island biogeography
One of the paradigms of the equilibrium theory of island biogeography as proposed by MacArthur and Wilson (1967) is that the immigration of species depends mainly on the distance to potential source regions, while the extinction rate depends on the size of the island. Brown and Kodric-Brown (1977) incorporated the "rescue effect" stating that extinction is also influenced by distance, whereas Lomolino (1990) highlighted that immigration is also influenced by island area ("target effect"). Later, Heaney (2000) and Lomolino (2000) came up with two theoretical models relating immigration, extinction and speciation. Both argue that with increased isolation, the immigration rate declines, while the speciation rate increases due to genetic isolation and unoccupied ecological niche space.

The Canary Islands
On the Canary Islands we encounter a unique situation compared to other oceanic archipelagos. Although there is some evidence for colonisation from other Macaronesian archipelagos through the Iberian Peninsula (Marshall and Baker 1999, Fernández-Palacios et al. 2011) it is realistic to assume that the North-western part of the African mainland has been an important source region for the Canarian biota; Fuerteventura is currently 95 km from the African coast, and was only 60 km apart during the last Glaciation, just 18 Ky ago (García-Talavera 1999). North Africa has been subjected to a progressive climatic deterioration over time, especially after the occurrence of several geological events in the Neogene. Among them are the closure of the corridor between the Indian and Atlantic Oceans, the closure of the Gibraltar strait leading to the Messinian salinity crisis, the arrival of Glaciation cycles and the onset of the Mediterranean climate in the Pleistocene bringing several desertification cycles to the Saharan region (Stanley 1999). These historic environmental conditions on the African continent might be more important for plant species diversity on the Canary Islands than present conditions, as many species might have migrated from the nearby continent in the past. Such importance of historic conditions for variation in plant species diversity on the Canary islands was also shown by Zobel et al. (2011) who find plant species diversity on the Canary islands to be strongly related to historic (pre human) habitat area and island age.
As the Moroccan-Saharan coastal plains are lowlands, immigrating species from this origin are adapted to low elevation ecosystems and will therefore occupy habitats and ecosystems in the low altitudes of the islands. The elevation on Gran Canaria, Tenerife, La Palma and El Hierro exceeds the Moroccan-Saharan coastal plains by far. Comparable elevations to the Pico de Teide (3718 m) only occur in the High Atlas Mountains of Morocco (Djebel Toubkal, 4167 m) at a distance of ca. 900 km. This substantially exceeds the distance from coast to coast. Thus, the distance from island ecosystems to ecosystems of similar environmental conditions increases with elevation (Figure 1a). As dispersal is dependent on distance, habitats placed at higher elevations on the islands are geographically more isolated from ecosystems of similar environmental conditions. Even if an equal number of diaspores or individuals of continental species may arrive in all elevation zones, most of them will very likely originate from geographically closer regions. As these diaspores would come from a low elevation ecosystem on the continent, most of those species will not be able to establish in high elevation ecosystems due to unsuitable environmental conditions. It has already been shown that directional ecological

filtering is very important for the colonisation of non-native species into high altitude regions worldwide, and this mechanism might be also working for native species (Alexander et al. 2011). Even though one has to be careful when comparing island and continental ecosystems (Figure 1b), the described mechanism results in a situation where many species occupy low elevations while the niche space available at higher elevations remains empty. This combination provides optimal conditions for diversification at the higher altitudes.

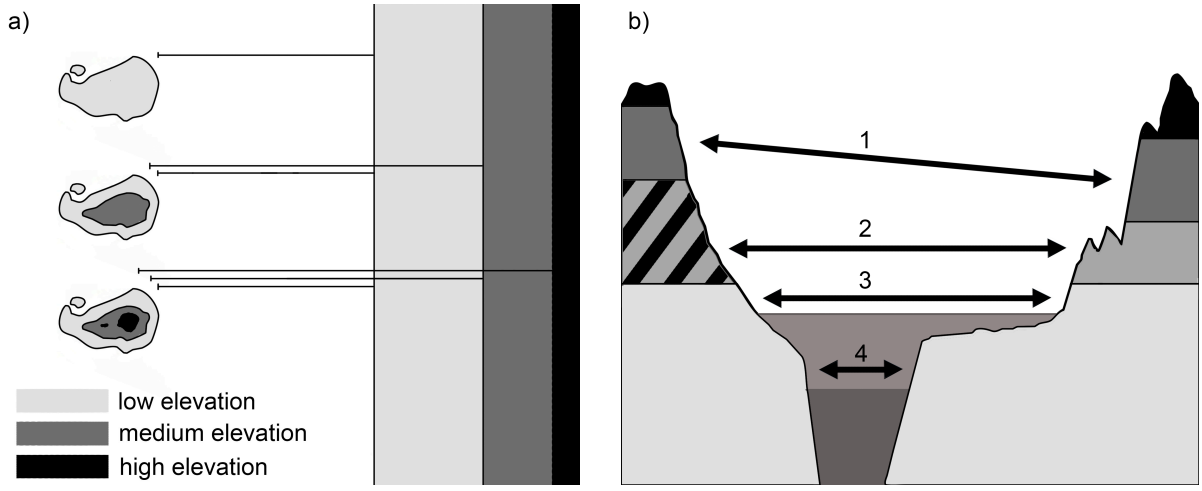

Figure 1. *Theoretical relationship between elevation and isolation on oceanic islands. (a) Isolation can be caused by elevation, as different geographical distances from the ecosystem on an island (left side) to its source region on the mainland (right side) have to be taken into consideration when ascertaining the distance a species has to cross to reach a suitable habitat on an island. If immigrating species are mainly adapted to low elevation ecosystems according to the altitudes of their nearby source region, they will leave habitats in high elevations unoccupied. This situation promotes in situ speciation in the high altitude ecosystems leading to a high percentage of endemic species. (b) However, when comparing islands (left side) with the mainland (right side), ecosystems are not necessarily associated with the same elevation range due to several reasons: (1) ecosystems might be situated at different elevation levels, due to a change in temperature gradients; (2) ecosystems of the same band might contain completely different species, due to changes in climatic or edaphic conditions; (3) although occasionally it can be assumed that these are similar across altitudes; and finally, (4) due to Pleistocene' sea surface fluctuations, neither elevation nor distance can be treated as being constant in time.*

Given the importance of both, available niche space and isolation for diversification rates, we can formulate two hypotheses:
H1. If speciation is driven by the availability of unoccupied niche space and enabled by isolation, it should increase with island elevation. pSIE, as an indicator for overall diversification, should follow this tendency. Both Pereira et al. (2007) and Emerson and Kolm (2007) agreed in that the identified correlation between species richness and the pSIE could be due to the influence of one variable driving both distribution patterns through different mechanisms. This variable might be island altitude; on the Canary Islands, elevation is correlated with environmental variations and thus habitat diversity (Steinbauer and Beierkuhnlein 2010), which in turn is correlated with island size. In addition to this, as mentioned before, high elevations form isolated areas where speciation may take place. However, if the species exchange between the islands of an archipelago is relatively high, it is likely that species evolving on one island also colonise another one, or that species do not evolve on one, but on several islands. In these cases the proportion of multi-island endemic species (i.e. species endemic to the archipelago) should increase with elevation.

H2. Processes and linkages identified by comparing islands within one archipelago should also be observable when comparing specific ecosystems that are present on these islands. This implies that for the different altitudinal ecosystems both the positive correlation between species richness and pSIE identified by Emerson and Kolm (2005b) and the hump-shaped relationship between island age and pSIE identified by Whittaker et al. (2007) should also be detected for inter- ecosystem relationships.

Methods

Canarian native seed plants (Spermatophyta) were assigned to the five major zonal ecosystems of the archipelago based on the literature (Izquierdo et al. 2004) and personal experience. "Potentially native species" were excluded to prevent errors. Altogether 932 species were included in the analysis. The distribution of main ecosystems on the Canary Islands follows an altitudinal gradient (see detailed description in Zobel et al. 2011). Roughly 60% of the species were assigned to one zonal ecosystem (including the main representatives of the different altitudinal ecosystems such as *Euphorbia canariensis* (subdesert coastal scrub), *Juniperus turbinata* (thermophilous woodlands), *Laurus novocanariensis* (laurel forest), *Pinus canariensis* (Pine forest) or *Spartocytisus supranubius* (subalpine scrub)), whereas ca. 40% of the species were found to have a larger altitudinal distribution, occurring in two to five zonal ecosystems depending on their ecological amplitude. Species occurring in more than one zonal ecosystem were therefore assigned to each ecosystem where they occur. This poses the problem of pseudoreplication, which we can only partly control for by including island as random effect in some of the calculations (see below). Analyses were restricted to those zonal ecosystems that actually occur on an island (n=25 and not 5x7=35). For instance, on Fuerteventura and Lanzarote, laurel forest, pine forest and subalpine scrub were not considered, as they do not exist on these islands. The percentages of singe-island endemics (pSIE) and multi-island endemics (pMIE; species endemic to the archipelago) were calculated for all zonal ecosystems on all islands (Table 1).

The potential (Holocene) altitudinal ranges for the ecosystems (Table 2) are not the same for the island's windward and leeward slopes and may vary among islands. While e.g. the pine forest extends around the islands, the laurel forest is limited to the islands windward slopes. Above the tree line of the pine forest we cannot find any distinction between the windward and leeward sides in the subalpine zone. Based on this, we considered the lowest limits of the ecosystems along the windward slope for the calculations, as all the zonal ecosystems are represented there (Table 2). The area covered by the elevation belts was estimated using the potential distribution of natural vegetation (del Arco Aguilar, 2006, Table 1d), assigning all vegetation types to the five major habitats defined for our study.

The increase of pSIE with elevation was tested using generalized linear mixed models with a binomial family error, testing for island as a random effect. The linear relation with elevation was also tested for pMIE. To assess the influence of area, additional models including island and habitat area (quadratic-, log- and untransformed) were compared to the afore-mentioned simpler models.

***Table 1**: a) Proportion of single island endemics b), proportion of multi-island endemic species (MIEs), c) number of native species and d) habitat area (in km²; rounder off), listed for specific ecosystems and islands. Those values that were not included in the calculation are in grey. H: El Hierro, P: La Palma, G: La Gomera, T: Tenerife, C: Gran Canaria, F: Fuerteventura, L: Lanzarote.*

1 a)	**H**	**P**	**G**	**T**	**C**	**F**	**L**	**TOTAL**
Coastal scrub	4.0	4.2	5.9	15.9	7.7	2.6	3.8	24.5
Thermophilous woodland	6.8	7.1	12.6	18.1	15.7	3.3	3.6	36.7
Laurel forest	2.8	8.4	5.3	8.8	6.7	-	-	21.9
Pine forest	1.8	13.2	-	10.9	24.8	-	-	34.4
Subalpine scrub	-	9.5	-	24.4	-	-	-	29.2
1 b)	**H**	**P**	**G**	**T**	**C**	**F**	**L**	**TOTAL**
Coastal scrub	27.8	29.8	30.9	26.6	23.9	19.8	19.5	23.7
Thermophilous woodland	28.6	31.8	30.2	31.5	25.3	21.2	19.0	26.1
Laurel forest	26.4	26.6	29.4	26.9	24.0	12.0	8.5	24.8
Pine forest	27.3	25.0	25.0	26.3	18.0	11.1	7.7	20.5
Subalpine scrub	21.2	34.9	14.3	31.7	27.9	4.1	4.0	29.2
1 c)	**H**	**P**	**G**	**T**	**C**	**F**	**L**	**TOTAL**
Coastal scrub	176	191	220	327	285	268	262	485
Thermophilous forest	147	154	182	238	198	151	137	349
Laurel forest	178	203	228	249	208	92	82	319
Pine forest	110	136	112	156	161	63	65	224
Subalpine scrub	33	63	35	82	43	24	25	89
TOTAL	340	415	432	626	533	345	323	932
1 d)	**H**	**P**	**G**	**T**	**C**	**F**	**L**	**TOTAL**
Coastal scrub	81	64	122	607	852	1626	824	4177
Thermophilous forest	69	153	137	359	203	27	18	967
Laurel forest	66	189	103	412	193	0	0	962
Pine forest	52	285	6	441	309	0	0	1092
Subalpine scrub	0	15	0	213	0	0	0	228
TOTAL	268	707	368	2033	1558	1657	845	7436

The postulated linear relationship between pSIE and species richness at the ecosystem scale was also evaluated using generalized linear mixed models with a binomial family error, testing for island or habitat or both as random effects, respectively. Island and habitat area (quadratic-, log- and untransformed) were additionally tested for influence. In a separate model, elevation and its interaction with species richness was included in the model with island as random effect.

To test whether the hump-shaped (unimodal) link of pSIE with age as reported for the inter-island scale (Whittaker et al. 2007, 2008) can also be identified for the inter-ecosystem scale, we compared two alternative generalized linear mixed models with a binomial family error testing for habitat as a random effect with and without age² as an additional predictor. As these ecosystems

***Table 2:** Potential altitudinal ranges (in meter) of the ecosystems as approximated for the Holocene. The lowest limits from the windward island side were considered for the linear correlation.*

	Windward	Leeward
Coastal scrub	0 - 300	0 - 400
Thermophilous woodland	300 - 600	400 - 700
Laurel forest	600 - 1200	-
Pine forest	1300 - 2000	700 - 2300
Subalpine scrub	2000 - 3000	

occur at similar elevations on all islands, altitude does not influence a possible relationship between pSIE and island age here. Again, the hypothesis was also assessed for pMIE. In addition, we tested the influence of island and habitat area (quadratic-, log- and untransformed) and included elevation and its interaction with the other predictors in those models with island as random effect. To refine the influence of habitat area on pSIE as well as pMIE, we tested models combing age and age^2 with log-habitat area and log-habitat area^2 with habitat as random effect.

All calculations were performed using the statistical program R (R Development Core Team 2010). We used package "lme4" version 0.999375-32 (Bates and Maechler 2009) for the generalised linear mixed effect models. Models were fitted using maximum likelihood, to enable a comparison between models with different fixed effects. Models were compared using ANOVA. See Bunnefeld and Phillimore (2011) for a discussion on the use of linear mixed models in island biogeography.
To visually assess possible differences in the relationship between island age and overall diversification between altitudinal zones, we plotted pSIE against island age for coastal scrub and thermophilous woodland ecosystems. We compared the resulting plots with the plots on the relationship between pSIE for the whole island and island age presented by Whittaker et al. (2007). These results were reproduced using data obtained from Izquierdo et al. (2004).
Following Whittaker et al. (2007), island age addresses the time span that has been available for immigration and diversification processes, which in most cases corresponds to the geological age. These authors suggest an age of 3.5 Myr for Gran Canaria assuming a volcanic eruption that sterilised the island (Marrero and Francisco-Ortega 2001). This assumption is criticized by Anderson et al. (2009) who propose an age of 14.5 Myr. We evaluate both hypotheses in our models. For Tenerife an age of 8 Myr was assumed, corresponding to the emersion of the three basaltic massifs that today form Tenerife's edges (Anguita et al. 2002).

Results
A significant (p=0.001) increase of pSIE with elevation was identified by the generalized linear mixed model with island as a random effect (Figure 2a; slope: 0.0003 ±0.0001; increase of pSIE ~ 0.01-0.04/km) (overview of model results in Table 3; slopes are always reported for binomial model with a logit link). There was no significant relationship between pMIE with elevation, species richness, habitat area or island area.
Both pSIE and species richness were found to be related on the ecosystem scale. Interestingly, we identified a positive relationship with habitat as random effect ($p<0.001$; figure 2c; slope: 0.0133 ±0.0015) but a negative relationship with islands as random effect ($p<0.01$; figure 2b; slope: -0.0029 ±0.0009). A positive relation was identified having both as random effects (p=0.03; slope: 0.0071 ±0.0023). Random effect variance estimates (intercept) are 0.2252 ±0.4745 for island and 0.6808 ±0.8251 for habitat, respectively. Including a term for the habitat area (quadratic- and untransformed) in the model with the habitat as random effect significantly increased model performance but did not affect the significance of species richness. The interaction of elevation and species richness was non significant.
We found evidence for the hump-shaped (unimodal) relationship between pSIE and island age (time available for speciation) postulated by Whittaker et al. (2007, 2008) (Figure 2d). Model performance increased significantly ($p<0.001$) when age^2 was included in the generalized linear mixed model with habitat as a random effect. The model parameter for age^2 is negative, resulting in the "humped" shape (slope age: 0.2435 ±0.0354, slope age^2: -0.0154 ±0.0021). We identified a significant interaction of elevation with age*** and age^2*. Area significantly increased model performance (log-habitat area $p<0.001$; island area $p<0.01$, log-island area $p<0.001$, island area^2 $p<0.05$) but did not question the significance of age or age^2. When habitat was treated as a random effect, log habitat area and log habitat area^2 were found to be significant predictors of pSIE (slope log habitat area: 3.0818 ± 0.5448, slope log habitat area^2: -0.2619 ±0.0512), rendering a hump shaped relationship (figure 2e). When coastal scrub was excluded from the analyses, the model supported a linear relation with pSIE, leaving log-habitat

area^2 non-significant. A combined model of log habitat area**, log habitat area^2*, age*** and age^2*** for all zonal ecosystems revealed all four predictors to be significant.

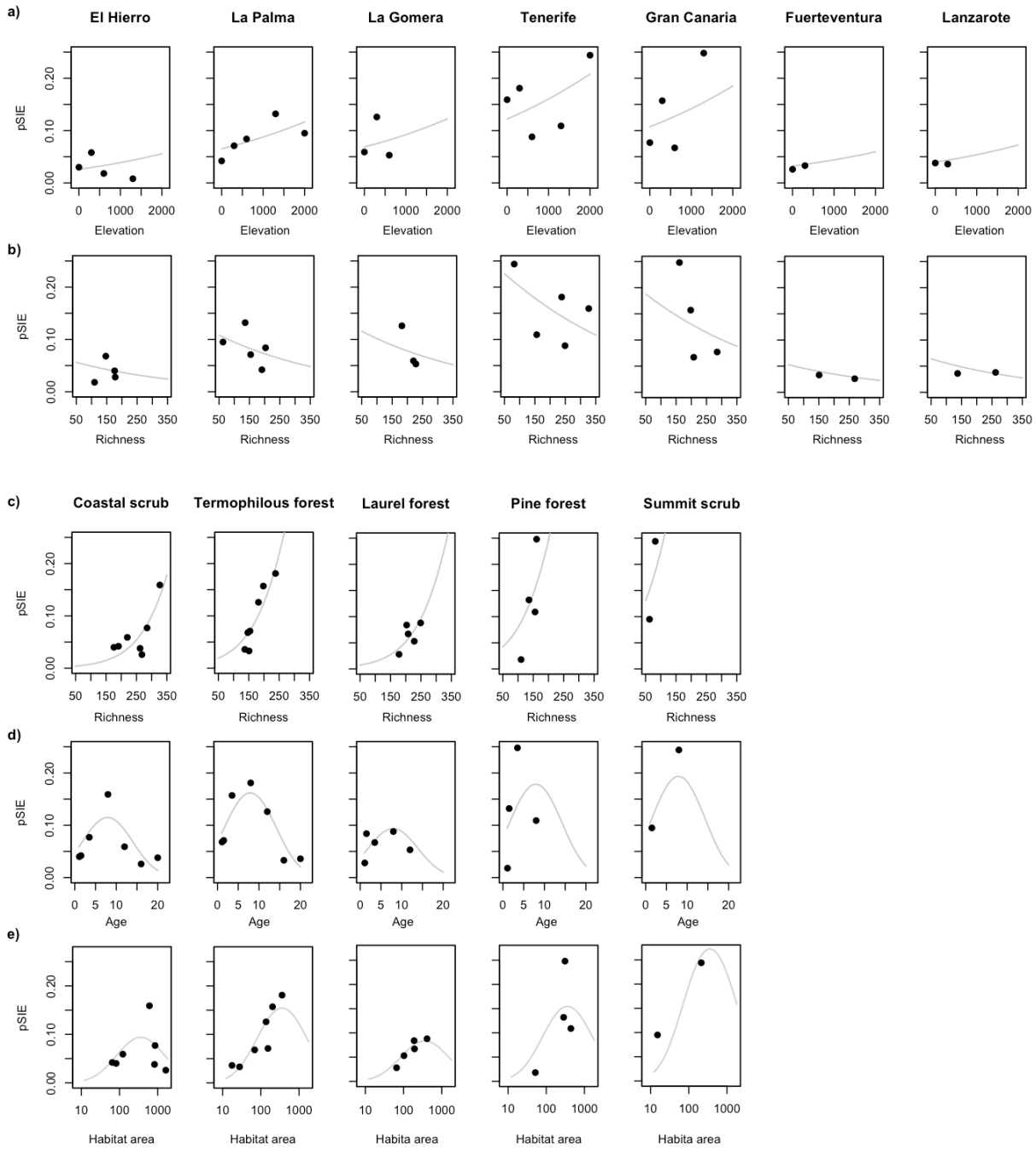

Figure 2. *Observed relationships between the percentage of Single Island Endemics and elevation. (a) The increase of pSIE with elevation could indicate an increase of speciation. (b) A decline of pSIE with species richness within islands can be seen as a logical result. However, within ecosystems on different islands both (c) a positive relation between species richness and pSIE and (d) a hump shaped relation between pSIE and age are observed. This is consisted with island scale analyses (comparing entire islands): (e) the relation of (log-)habitat area with pSIE is also hump shaped, but becomes linear if coastal scrub is removed from the analysis (not shown). The grey line indicates model predictions as derived from general mixed effect models integrating either all islands or habitats, in one analysis.*

The relationship between pMIE and age was also "hump-shaped" as indicated by a significantly ($p<0.01$) increased model performance after including age^2 (slope age: 0.0385 ±0.0201, slope age^2: -0.0029 ±0.0010). Model performance was additionally enhanced after including habitat area or island area (Table 3). Log habitat area and log habitat area^2 significantly explained pMIE (slope log ha. area: 0.6888 ±0.2331, slope log ha. area^2: -0.0722 ±0.0222) when habitat was a random effect. Significance of log habitat area and log habitat area^2 was lost after including age* and age^2** as additional predictors.

Assuming an age of 14.5 Myr (instead of 3.5 Myr) for Gran Canaria, the hump-shaped (i.e. uni-modal) relationships with age of pSIE and pMIE remained significant (not shown in Table 3). These results can be clearly seen in Figure 3a where for the ecosystems of "coastal scrub" and "thermophilous forest" pSIE follows a hump-shaped relationship with island age, consistent with the findings of Whittaker et al. (2007) on an island scale (Figure 3b). The smaller ratios for pSIE in Figure 2b compared to Figure 3a result from the overall smaller number of species within our data set that is ecosystem-specific for Spermatophyta compared to the one provided by Izquierdo et al. (2004).
We also identified a surprisingly high percentage of SIE in the "thermophilous forest" that is consistent for most islands of the Canarian archipelago except for La Palma and Lanzarote (Table 1a). The same pattern emerged with different ratios when looking at the pMIE (Table 1b). Here, even La Palma had a second maximum in the ecosystem of the "thermophilous forest". Overall, species numbers decline with elevation (Table 1c).

Discussion

The existence of a general increase of pSIE with altitude (our Hypothesis 1) is supported by our results, which indicate increasing diversification rates with elevation. We suggest that species inhabiting high altitude ecosystems on islands are genetically more isolated than their low elevation counterparts due to a larger spatial distance to comparable ecosystems (and thus lower immigration rates of potential colonisers –many diaspores of species that are not able to establish viable populations in high elevations may still arrive). This is supported by Zobel et al. (2011), who found the number of ancient immigrants in high elevation ecosystems on the Canary Islands to be smaller than expected from habitat area and island age. *In situ* speciation caused by the availability of ecological niches within the isolated high elevation ecosystems is, however, only one among other influential factors for SIE on island archipelagos. The heterogeneity within the data indicates that other factors such as the temporal availability and the spatial extent of ecosystems, the disturbance regimes, the geological evolution of specific islands [with sterilization (Gran Canaria), coalescence (Tenerife) or fragmentation (Lanzarote-Fuerteventura) events] and, last but not least, the properties of the specific species will all majorly contribute to species distribution on these island systems. In addition, Whittaker et al. (2007, 2008, 2010) highlight the importance for directed intra-island species colonisation from older islands to the new, recently emerged, one. This process includes already submerged islands and can thus be much older than the present archipelago (Fernández-Palacios et al. 2011). Steinbauer and Beierkuhnlein (2010) found strong indication that for the Canary Islands within-island species exchange is more important than external immigration, although the latter process does also occur. As distances between the same habitats on different islands are similar, elevation could produce a target area effect for inter-island exchange, with smaller areas in the top regions. Larger areas would thus increase immigration rate and reduce speciation rate through genetic mixing and occupation of niche space. However, area is in general thought to increase speciation rates (Losos and Schluter 2000; Kisel and Barraclough 2010), which is also supported by the detected significant positive influence of habitat area on pSIE. It has been shown that for habitat specialists the relation between diversification and age may even be the opposite of the general trend if the associated habitat area varies different then the overall island area (Borges and Hortal 2009). In addition, the hypothesised "elevation-driven isolation" is a process that is not only affecting single islands but also the archipelago as a whole. Some of

the present summit scrub vegetation has probably migrated from Lanzarote and Fuerteventura to Tenerife and La Palma. Nonetheless, the summit scrub vegetation on all these islands is relatively isolated in respect to continental habitats of similar environmental conditions and the colonisation of new species is thus less likely than on less elevated ecosystems. The high elevation ecosystems remain poorer in species and leave ecological space for speciation. Even if this process might not apply to all species or is altered by several environmental influences, the geographic distance to (now or in the past) habitats with similar ecology on the nearby continent or adjacent archipelagos will influence the immigration and speciation processes.
A significant decrease of pSIE with species richness when comparing habitats on islands (with island as a random effect) would be expected from an increase of pSIE with elevation and a concordant decrease in species richness in smaller high elevation ecosystems. As a consequence for the island scale (i.e. comparing entire island data sets), this can lead to a fortuitous positive correlation of the two variables as larger islands tend to have more species (in general) and a higher pSIE due to high elevation ecosystems. Surprisingly, a pattern of a positive relationship between species richness and pSIE (as an indicator for diversification) was identified when comparing the same ecosystems on different islands (with habitat as a random effect). This analysis excludes elevation. A positive correlation between species richness and habitat area might be a possible cause.

Table 3. *a) Model performance of the generalized linear mixed models with binomial family errors. Note that the model did not use percentage values as dependent variables but binomial proportions (SIE, n.spec-SIE). b) Smaller AIC values after including area as an additional predictor indicate better model performance. Significance of the additional predictor (area) is indicated with the AIC values (p<0.05*, p<0.01**, p<0.001***). Note that including area into the model never questioned the significance of the original predictor(s).*

a) original model					**b) original model + additional predictor**					
dep.	predictors	random	model p-value	AIC model	AIC +habitat area	AIC +log (habitat area)	AIC +habitat area^2	AIC +island area	AIC +log (island area)	AIC +island area^2
pSIE[1]	~elevation**	island	0.001	96.1	97.6$^{n.sig.}$	97.4$^{n.sig}$	96.5$^{n.sig.}$	96.4$^{n.sig}$	96.7$^{n.sig}$	99.4$^{n.sig}$
pSIE[1]	~richness**	island	0.002	96.5	98.5$^{n.sig.}$	95.1$^{n.sig}$	98.2$^{n.sig.}$	96.5$^{n.sig}$	96.9$^{n.sig}$	96.1$^{n.sig}$
pSIE[1]	~richness***	habitat	<0.001	93.3	81.0***	95.2$^{n.sig}$	78.0***	95.2$^{n.sig}$	95.1$^{n.sig}$	95.2$^{n.sig}$
pSIE[1]	~time*	habitat	0.017	160.8	not tested	not tested	not tested	not tested	not tested	not tested
pSIE[1]	~time*** +time^2 ***	habitat	<0.001	95.4	96.1$^{n.sig}$	84.3***	96.7 $^{n.sig.}$	86.6***	83.3***	89.1**
pMIE[1]	~time**	habitat	0.006	41.0	not tested	not tested	not tested	not tested	not tested	not tested
pMIE[1]	~time$^{n.sig.}$ +time^2**	habitat	<0.001	35.2	30.3**	30.5**	32.4*	28.1**	28.3**	29.5**

We also confirm for the ecosystem scale that the relationship between pSIE and island age is hump-shaped, as predicted by the general dynamic theory of oceanic island biogeography (Whittaker et al. 2008). This rejects the influence of island elevation as a possible covariable for island age (Steinbauer and Beierkuhlein 2010). Given the typical ontogenesis of oceanic islands (Whitaker et al. 2007), we would expect island age and elevation to be inversely related. An ageing island is likely to become flatter. In addition, both elevation and age are said to influence island complexity (as a surrogate for carrying capacity) (Whitaker et al. 2007, 2008). It has been shown that working on the ecosystem scale can be a successful way of differentiating both variables. Testing possible implications of the general dynamic theory of oceanic island biogeography for ecosystems placed at similar altitudes on the same or different archipelagos bears promising future research opportunities.
Whittaker et al. (2008) and Triantis et al. (2008) suggest an important influence of area: on average the area threshold for SIEs is larger than that for MIE and non-endemic species. That is

to say that MIEs and non-endemic species are more likely to persist even as fairly small populations due to an occasional influx of individuals from other islands, that has been referred to in the past as the rescue effect (Brown and Kodric-Brown 1977). Price (2004) showed for the Hawaiian Islands that the influence of area in defining diversity patterns is strong, also for pSIE and habitat types. One would assume that the smaller area of the subalpine scrub ecosystem probably also influences the presence of species groups, especially native non-endemics and MIE, reflected by the decline in the number of MIE as well as non-endemic species with altitude. Habitat area has a stronger effect on pSIE with habitat as random effect than with island as random effect. The main reason for this is probably that habitat area is strongly linked to island area and thus variation within one island is lower than between the islands. With habitat as random effect, habitat area follows a linear relation with island age that becomes hump shaped if the coastal shrub is included in the analysis (Figure 2e). It seems that speciation tends to increase with habitat area, but this relation is altered in the lowland ecosystems that especially increase in area in old stages of an island. Area has also been cited as a main factor triggering speciation and the relation is suggested to be not linear with threshold area values for accelerating speciation rates (Losos and Schluter 2000). Thus, it is likely that a particular habitat type on an island needs to reach a certain size for triggering speciation. A further increase of habitat area will then lead to increasing speciation rates. An alternative explanation for an area threshold is an increased extinction rate. If an area is too small, only few lineages will survive for long enough to be recognised as species (Rosindell and Phillimore 2011). In many cases habitat area will be correlated with age in the beginning of island evolution, which makes a differentiation of both variables difficult. On old islands habitat size seems to be of less importance for speciation, probably because the availability of empty niche space is reduced due to species pool saturation and decreasing altitude and topographical complexity.

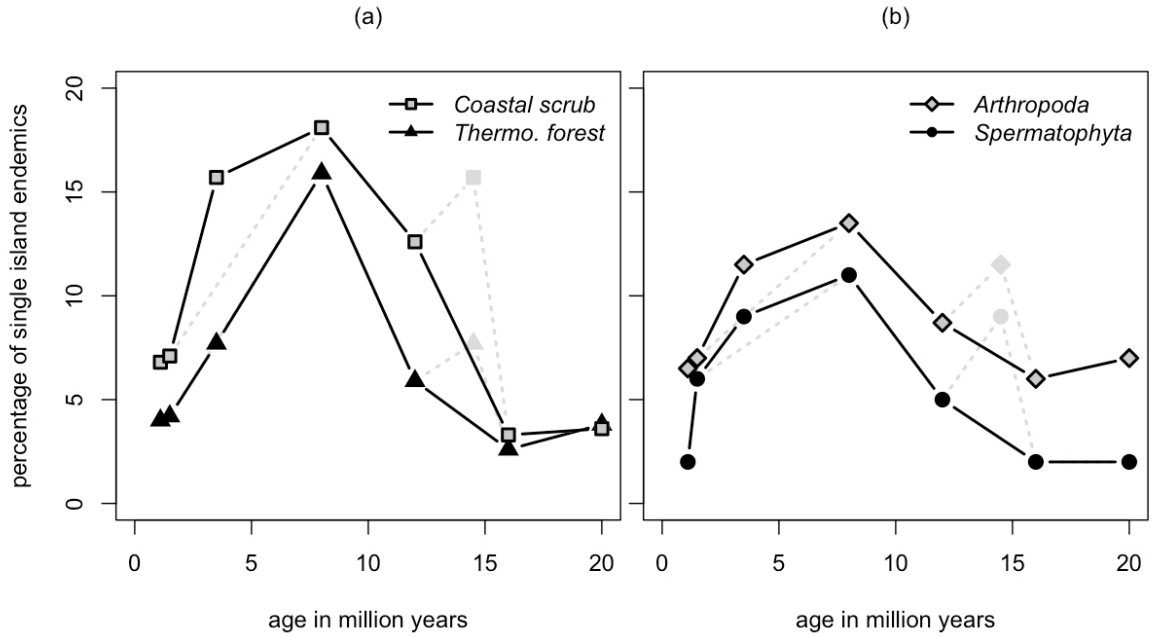

Figure 3. *(a) For the ecosystem scale the relation of pSIE with island age resembles a hump shaped curve as suggested by the "island immaturity speciation pulse model" in Whittaker et al. (2007). (b) On an inter-island scale the curve for pSIE and age used by Whittaker et al. (2007) is flatter. If an age of 14.4 million years is assumed for Gran Canaria as suggested by Anderson et al. (2009) instead of 3.5 million years as assumed by various authors following Whittaker et al. (2007), the curves would change as indicated by the grey dotted lines.*

The habitat types used here vary in age. Several of them are younger than the old islands (thermophilous woodlands, coastal scrub, summit scrub). The pine forest and Laurel forest can be considered old ecosystems since fossils for *Pinus canariensis* are dated 13 Myr on Gran

Canaria (García-Talavera et al. 1995, Domínguez et al. 2010). The low elevation ecosystems seem to be younger or their species composition has entirely changed. However, there are several reasons why we decided to focus on island age. Fist, the species (or their ancestors) living in a specific habitat might be older than the habitat type. Second, in the Whittaker et al. (2008) model (that is our reference in this aspect) age is the time that was available for species to colonisation or speciation. This time is constrained either by the islands age or any sterilising mega event. In case of habitat types this becomes very complicated, because climatic fluctuations might shift the spatial position of the climatic envelope of a current habitat type, however, the species in this habitat might be different in their climatic sensitivity leading to a mixture or rearrangement of species communities with time. Third, island age is not only the time available for speciation, but also a surrogate for some other characteristics (like e.g. complexity). The fact that we found a relation on the habitat level with island age is a strong indicator that the role of age in the model is currently not understood but probably crucial for a further progress in island biogeographical theory.

Triantis et al. (2008) highlight cases that might flaw SIE as an indicator for *in situ* speciation. There are three points where endemism might not only evolve from intrinsic factors of the island, but also from extrinsic ones. Firstly, SIE might have evolved but already gone extinct. However, if the extinction of previously evolved SIE is as probable as the extinction of previously immigrated species, these cases will not influence the distribution pattern of pSIE. However, SIE might be more likely to survive, as in order to speciate a population has to persist for a long time and, presumably, be relatively abundant. If this hypothesis is valid it is probably equally applicable to all islands and habitats. Secondly, SIE can lose their status and turn into "only" MIE by colonising a second island within the archipelago. However, the consistent distribution pattern for pMIE and pSIE and the fact that archipelago endemism is also linked to speciation supports the connection of diversification to pMIE, pSIE and elevation. MIE on the other hand can also become "false SIEs" –a case that was not mentioned by Triantis et al. (2008). This could take place in particular as a result of human extinction pressure leading to the disappearance of MIEs on all islands except one. Finally, Triantis et al. (2008) mentions that ancient immigrants might have become extinct in the region of their origin (palaeoendemism). This point is particularly valid for the Canary Islands, where a lot of species in the main source region (mainland Africa) might have gone extinct due to climatic changes (Axelrod 1975, Le Houerou 1997). However, these species should mainly be distributed in the low to mid elevation ecosystems, due to the corresponding elevation of the source region, and are therefore more likely to be MIE than SIE, as successfully immigrating species should be able to colonise more than one island.

An extinction of species on mainland Africa could be a possible explanation for the relatively high values for pSIE and pMIE within thermophilous woodland. Some of the species found at low and mid altitudes might be remnants of species that survived the climatic ice age fluctuations only on the Canary Islands, while becoming extinct on the African mainland. Lowland ecosystems might have survived glaciations due to an upward shift, which was not possible for high elevation ecosystems. However, laurel and pine forests are supposed to be older than other Canarian ecosystems. This is especially true for the thermophilous woodlands that are comparable to Mediterranean sclerophyll forests (Fernández-Palacios et al. 2009). It is suggested that these ecosystems substituted the former palaeotropical flora of Southern Europe and North Africa in the late Miocene and Pleistocene periods (Axelrod 1975, Barrón and Pierrot 2006). The thermophilous woodland constitutes the zonal ecosystem that was most disturbed by anthropogenic activities both in the prehistoric (i.e. through fire, introduced goats and pigs) and historic periods (i.e. with settlements and agriculture) (Fernández-Palacios et al. 2009). One could argue that land use practises together with the resulting small-scale disturbance regime might have formed a heterogeneous landscape where *in situ* diversification was not only triggered by environmental complexity but also by extinction pressure. However, an explanation for the high values of pSIE based on human influence is very unlikely as the Canary Islands

were only colonised by man 2500 years ago (de Nascimento et al. 2009) and practically all SIE in this habitat are shrub species.

Conclusions

Our results add valuable insights for an improved understanding of island archipelago systems. We were able to show that pSIE (and thus diversification) is linked to the elevation of an ecosystem. This is probably caused by an increasing spatial isolation of elevated ecosystems on an island. It may serve as an additional explanation for a hypothetical fortuitous correlation between pSIE and the species number on an island scale (Emerson and Kolm 2005). However, we identified the same correlation on the ecosystem scale, possibly caused by a correlation between species richness and habitat area.

The general dynamic theory of oceanic island biogeography (Whittaker et al. 2007, 2008) postulates a certain correlation between island elevation and complexity (indicator for vacant ecological niches) triggered by island age. But as pSIE even within the same ecosystems on different islands follows a hump-shaped relationship with island age (Figure 2a), the importance of island age (or the time available for diversification) is stressed as an independent factor. Diversification is also related to habitat area, a factor that seems to be of special importance on young islands.

These insights support the results of current island biogeographical theories for different spatial scales, opening up new opportunities for future scientific focus and discussion. Further application of island-specific theory at the habitat level will not only result in a promising new insight but will also be much easier to perform (in case that habitat types can be defined) than studies on the island scale.

Acknowledgements

We would like to thank Joaquín Hortal, Christoph Kueffer, Albert Phillimore, Björn Reineking and the anonymous reviewers for very valuable comments and advice.

References

Alexander, J.M., et al. 2011. Assembly of nonnative floras along elevational gradients explained by directional ecological filtering. P. Natl. Acad. Sci. USA 108: 656-661.

Anderson, C.L. et al. 2009. Life, death and fossilization on Gran Canaria – implications for Macaronesian biogeography and molecular dating. - J. Biogeogr. 36: 2189–2201.

Anguita, F. et al. 2002. Los Volcanes de Canarias. Guía Geológica e Itinerarios. - Ed. Rueda, Madrid.

Axelrod, D.I. 1975. Evolution and biogeography of Madrean - Tethyan sclerophyll vegetation. - Ann. Mo. Bot. Gard. 62: 280-334.

Barrón, E. and Pierrot, D. 2006. La vegetación forestal en el Terciario. - In: Carrión, J. et al.(eds.),Paleoambientes y cambio climático. Fundación Séneca / Agencia de Ciencia y Tecnología de la Región de Murcia, Murcia. pp. 55–76.

Bates, D. and Maechler, M. 2009. lme4: Linear mixed-effects models using S4 classes. - R package version 0.999375-32.

Birand, A. and Howard, D.J. 2008. The relationship between proportion of endemics and species diversity on islands: expectations from a null model. - Ecography 31: 286–288.

Borges, P.A.V. and Hortal, J. 2009. Time, area and isolation: Factors driving arthropod speciation at the Azorean Archipelago. - J. Biogeogr. 36: 178-191.

Brown, J.H. and Kodric-Brown, A. 1977. Turnover rates in insular biogeography - Effects of immigration on extinction. - Ecology 58: 445–449.

Bunnefeld, N. and Phillimore, A.B. 2012. Island, archipelago and taxon effects: mixed models as a means of dealing with the imperfect design of nature's experiments. - Ecography 35: 15–22.

Cadena C.D. et al. 2005. Is speciation driven by species diversity? - Nature 438: E1-E2.

del Arco Aguilar, M.J. 2006. Mapa de Vegetación de Canarias. - Grafcan, Santa Cruz de Tenerife.

de Nascimento, L. et al. 2009. The long term ecology of the lost-forests of La Laguna. - J. Biogeogr. 36: 499-514.

Domínguez, F. et al. 2010. Using taxonomic and phylogenetic evenness to compare diversification in two Island Floras. Perspect. Plant Ecol. Evol. Syst. 12: 93-106.

Emerson, B.C. and Kolm, N. 2005a. Species diversity can drive speciation. - Nature 434: 1015–1017.

Emerson, B.C. and Kolm, N. 2005b. Is speciation driven by species diversity? - Reply. - Nature 438: E2.

Emerson, B.C. and Kolm, N. 2007. Response to comments on "Species diversity can drive speciation". - Ecography 30: 334–338.

Fernández-Palacios, J. M. et al. 2009. Los bosques termófilos de Canarias. - Cabildo Insular de Tenerife, Santa Cruz de Tenerife.
Fernández-Palacios, J. M. et al. 2011. A reconstruction of Palaeo-Macaronesia, with particular reference to the long-term biogeography of the Atlantic island laurel forests. - J. Biogeogr. 38: 226–246.
García-Talavera, F. et al. 1995. Vegetales fósiles en el complejo traquítico-sienítico de Gran Canaria. Revista de la Academia Canaria de Ciencias, 7, 77–91.
García-Talavera, F. 1999. La Macaronesia. Consideraciones geológicas, biogeográficas, y paleoecológicas. - In: Fernández-Palacios, J.M. et al. (eds.) Ecología y cultura en Canarias. Cabildo Insular de Tenerife, pp. 39-63.
Gruner, D.S. et al. 2008. Does species richness drive speciation? A reassessment with the Hawaiian biota. - Ecography 31: 279–285.
Heaney, L.R. 2000. Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography. - Global Ecol. Biogeogr. 9: 59–74.
Izquierdo, I. et al. (eds.) 2004. Lista de especies silvestres de canarias - Hongos, plantas y animales terrestres. - Consejería de Política Territorial y Medio Ambiente Gobierno de Canarias, La Laguna, Tenerife, 2ª Ed.
Kiflawi, M. et al. 2007. Species diversity can drive speciation: comment. - Ecology 88: 2132–2135.
Kisel, Y. and T. G. Barraclough 2010. Speciation has a spatial scale that depends on levels of gene flow. Am. Nat. 175: 316-334.
Le Houerou, H.N. 1997. Climate, flora and fauna changes in the Sahara over the past 500 million years. - J. Arid Environ. 37: 619–647.
Lomolino, M. 1990. The target area hypothesis: the influence of island area on immigration rates of non-volant mammals. - Oikos 57: 297-300.
Lomolino, M.V. 2000. A call for a new paradigm of island biogeography. - Global Ecol. Biogeogr. 9: 1–6.
Losos, J.B. and Schluter, D. 2000. Analysis of an evolutionary species–area relationship. - Nature 408: 847–850.
MacArthur, R.H. and Wilson, E.O. 1967. The Theory of Island Biogeography. – Princeton University Press, Princeton, NJ.
Marrero, A. and Francisco-Ortega, J. 2001. Evolución en islas: la metáfora espacio-tiempo-forma. - In: Fernández-Palacios, J.M. and Martín, J.L. (eds.) Naturaleza de las Islas Canarias. Ecología y Conservación. - Turquesa, 2ª Ed. pp: 133-140.
Marshall, H.D. and Baker, A.J. 1999. Colonization history of Atlantic island common chaffinches (*Fringilla coelebs*) revealed by mitochondrial DNA. - Mol. Phylogen. Evol. 11: 201-212.
Pereira, H.M. et al. 2007. Does species diversity really drive speciation? - Ecography 30: 328-330.
Presgraves, D.C. and Glor, R.E. 2010. Evolutionary biology: Speciation on islands. - Curr. Biol. 20: 440-442.
Price, J.P. 2004. Floristic biogeography of the Hawaiian Islands: influences of area, environment and paleogeography. - J. Biogeogr. 31: 487-500.
R Development Core Team 2010. R: A language and environment for statistical computing. - R Foundation for Statistical Computing, Vienna, Austria.
Rosindell, J. and Phillimore, A.B. 2011. A unified model of island biogeography sheds light on the zone of radiation. Ecol. Lett. 14: 552-560.
Stanley, S. 1999. Earth System History. - Freeman, New York.
Steinbauer, M.J. and Beierkuhnlein, C. 2010. Characteristic pattern of species diversity on the Canary Islands. - Erdkunde 64: 57-71.
Triantis, K.A. et al. 2008. Evolutionary species-area curves as revealed by single-island endemics: insights for the inter-provincial species-area relationship. -Ecography 31: 401–407.
Vilenkin, B.Y. et al. 2009. A random process may control the number of endemic species. - Biologia 64: 107-112.
Whittaker, R.J. et al. 2007. The island immaturity - speciation pulse model of island evolution: an alternative to the "diversity begets diversity" model. - Ecography 30: 321–327.
Whittaker, R.J. et al. 2008. A general dynamic theory of oceanic island biogeography. - J. Biogeogr. 35: 977–994.
Whittaker, R.J. et al. 2010. A general dynamic theory of oceanic island biogeography: extending the MacArthur-Wilson theory to accommodate the rise and fall of volcanic islands. – In: Losos, J.B., Ricklefs, R.E. (eds.) The Theory of Island Biogeography Revisited. Princeton University Press, Princeton, pp. 88-115.
Witt, C.C. and Maliakal-Witt, S. 2007. Why are diversity and endemism linked on islands? - Ecography 30: 331–333.
Zobel, M. et al. 2011. The formation of species pools: historical habitat abundance affects current diversity. - Global Ecol. Biogeogr. 20: 251–259.

4. Manuscript 3 - Characteristic Pattern of Species Diversity on the Canary Islands

Erdkunde 64 (2010) DOI: 10.3112/erdkunde.2010.01.05

Manuel Jonas Steinbauer, Carl Beierkuhnlein

Summary: We use an island specific presence/absence data set for the Canary Islands' *Arthropoda*, *Spermatophyta*, *Fungi*, *Lichenes*, *Bryophyta*, *Mollusca*, *Chordata*, *Pteridophyta*, *Annelida* and *Nematoda* to assess the relative influence of environmental and historical factors on species distribution and endemism. Species richness and the percentage of island endemic species as well as similarity indices for island comparisons were calculated for all species groups. Hierarchical partitioning is used to identify the independent and joined influence of 21 environmental and historical variables. The pattern of species richness is best explained by island elevation. Elevation reflects a variety of factors that contribute to habitat diversity. A similar pattern is detected for the "percentage of single island endemics" (pSIE), a factor associated with speciation. Variables associated with geographical distance have highest explanatory power for biotical similarity of islands. Various Canary Islands species groups show strong distance-decay within the archipelago. According to our findings, speciation is not necessarily driven by species richness or island age alone. Thus, we conclude that correlations between species richness and pSIE, identified in previous studies, could represent an artefact related to differing degrees of isolation between zonal altitudinal ecosystems. This would lead to an increase of speciation with altitude resulting in higher values for pSIE on high altitude islands.

Keywords species turn-over, species–area, beta-diversity, alpha-diversity, Macaronesia, distance decay, Atlantic Ocean, island biogeography, speciation

1. Introduction

Ecological and evolutionary processes operate in overlapping spatial and temporal dimensions (Carroll et al. 2007; Fussmann et al. 2007; Kinnison; Hairston 2007). Heaney (2000) demonstrates that migration, extinction, and phylogenesis can be effective within comparable time spans. Therefore, it is difficult to differentiate the most influential processes responsible for the present pattern of species distribution. Simplified assumptions in popular biogeographical concepts, like the idea of equilibrium, have been proven to be wrong (see Brown and Lomolino 2000; Whittaker 2000; Heaney 2007; Whittaker and Fernández-Palacios 2007). In contrast to the suggestions made by MacArthur and Wilson (1967), immigration and extinction are not necessarily continuous processes, but can occur in the context of discrete events ("taxon pulses") (Ricklefs and Bermingham 2002; Halas et al. 2005).

The identification of variables that control processes and patterns in ecological systems is of major concern (Heaney 2007; Whittaker et al. 2007). The understanding of ecological processes in isolated regions, such as fragmented landscapes or patchy ecosystems, can profit from the research on island ecosystems (Duarte et al. 2008). By studying drivers for floristic richness on island ecosystems, various authors contributed to an improved understanding of global patterns of biodiversity (e.g. Morrison 2002; Willerslev et al. 2002; Price 2004; Roos et al. 2004; McMaster 2005; Panitsa et al. 2006; Dapporto and Dennis 2008; Duarte et al. 2008; Hannus and von Numers 2008).

The mere area of potential habitats is an important, albeit indirect, physical parameter that can be used to analyse patterns of species distribution (McMaster 2005; Whittaker and Fernández-Palacios 2007). For many archipelagos, a certain correlation of area with species number is documented (e.g. Price 2004; Roos et al. 2004; McMaster 2005; Duarte et al. 2008; Hannus and von Numers 2008). This linkage was even said to be one of the most powerful "rules" in ecology (Lomolino 2000b; Tjorve 2003; Triantis et al. 2003). Nevertheless, the functional background of this pattern is manifold and can hardly be traced precisely due to ecological complexity. Various explanations are under debate. The "habitat diversity hypothesis" (Williams and Bonsor 1964) assumes that a larger area, due to its supposed spatial heterogeneity, is connected with the conditional probability of hosting more species. According to the "area per se" hypothesis (Preston 1960; MacArthur and Wilson 1967) larger areas host more species, as the extinction risk of local populations is reduced on larger surfaces. Furthermore, according to the "passive sampling hypothesis" (Connor and McCoy 1979) and the "target area hypotheses" (MacArthur and Wilson 1967), the chance of an area to be colonised by locally "new" species increases with its size. The relevance of proximity is highlighted by the "rescue hypothesis" (Brown and Kodric-Brown 1977). It predicts declining populations or species that do not surpass minimum viable population sizes to be maintained when large and viable populations are close by and individuals or diaspores can disperse. This dynamic directly refers to the "source sink theory" for metapopulations introduced by Pulliam (1988). According to this concept, (large or suitable) habitat patches with population growth beyond their capacity contribute to the maintenance of habitat patches that can not sustain permanent viable populations. For general overviews see Triantis et al. (2003), Roos et al. (2004), Beierkuhnlein (2007) and Whittaker and Fernández-Palacios (2007).

Investigating a spectrum of physical and historical factors may reveal the processes behind single explanatory variables such as area. Such an approach has to be designed in a manner that allows assessing whether species richness, despite being correlated with area ("area per se" hypothesis), could be explained by parameters associated with habitat diversity ("habitat diversity hypothesis"). The "passive sampling -", the "target area -", the "rescue hypothesis" and the "source-sink theory" are more associated to an island's isolation from the target species source region. In this case, spatial filters like distance might be more important by reducing the probability of migratory and dispersal success.

Hannus and von Numers (2008) find both island area and habitat diversity to be correlated with species richness for an island archipelago in south-western Finland. For Mediterranean islands, Schmitt (1998) identified a linear increase in the number of taxa in ferns and flowering plants

with elevation and log(area). Including endemic species can provide information on speciation processes. For the west Italian islands, Dapporto and Dennis (2008) confirm the influence of distance to the nearest landmass source on species assemblage, species richness and endemism.
In this study, we test whether the number of species on an island and the dissimilarity in the species pool of islands are predominantly determined by ecological or spatial factors. The ecological background and the availability and heterogeneity of habitats directly control resource availability and ecological niches. It can be assumed that this is more important for species diversity than spatial or temporal qualities, which are considered in traditional island biogeography (Beierkuhnlein 1998). Habitat conditions are characterized in our study by a set of variables such as soil traits, geology, precipitation, temperature, forest cover, human population, inclination and elevation. A second group of variables was selected with focus on geographical aspects related to an island's isolation (distance to Africa, distance to next island, human induced connectivity, mean distance to the islands in the archipelago). In the following, the first group of variables is referred to as the 'ecological setting' and the second group of variables as the 'spatial setting'. As discussed above, area (active surface) could be associated with both categories. In addition, the historic factors "time" (available for evolution and immigration) and "age" of the island (existence) are analysed and discussed. These two terms are not necessarily exchangeable.

We hypothesize that species number is predominantly controlled by ecological settings and not by spatial settings (H1). Therefore, physical factors representing habitat diversity should explain more of the variance of the species richness patterns than isolating spatial parameters. Comparable analyses were applied for other archipelagos (e.g. Morrison 2002; Willerslev et al. 2002; Price 2004; Roos et al. 2004; McMaster 2005; Panitsa et al. 2006; Dapporto and Dennis 2008; Duarte et al. 2008; Hannus and von Numers 2008). Besides methods applied in these studies, similarity indices for beta diversity are calculated for the Canarian flora and fauna. We test if similarity in species compositions ("differentiation diversity" sensu Jurasinski et al. 2009) between the islands of the Canary Archipelago is more influenced by environmental isolation (species from a source region do not find suitable habitats) and less by spatial isolation (these species can not reach suitable habitats on the island) (H2). This is the first time, the relationship between distance in environmental parameters and similarity of species composition has been investigated on oceanic islands.

2. Study area

The Canary Islands are located near the African coastline between 27° and 29° northern latitude and 14° and 18° western longitude. The archipelago is of volcanic origin and consists of seven main islands larger than 250 km^2 (from east to west: Lanzarote, Fuerteventura, Gran Canaria, Tenerife, La Gomera, La Palma and El Hierro, see Figure 1). Five smaller islets (between 1 and 30 km^2) are not objects of this study. The oldest basalt shield of the island group in Fuerteventura rose around 20 million years ago over the sea surface. However, the formation of the submarine parts started already 70 to 80 million years ago (Anguita et al. 2002; compare Figure 1). 16 million years ago, the first parts of the subsequent island of Lanzarote emerged ("Femes"). The next islands to appear were Gran Canaria (14 million years), La Gomera (12 million years) and Famara (10 million years). The basalt blocks Teno, Adeje and Anaga rose around 8 million years ago. They fused together to one single island 1.5 million years ago and now form the edges of Tenerife. La Palma and El Hierro emerged rather late, 1.5 and 1.1 million years ago, respectively.

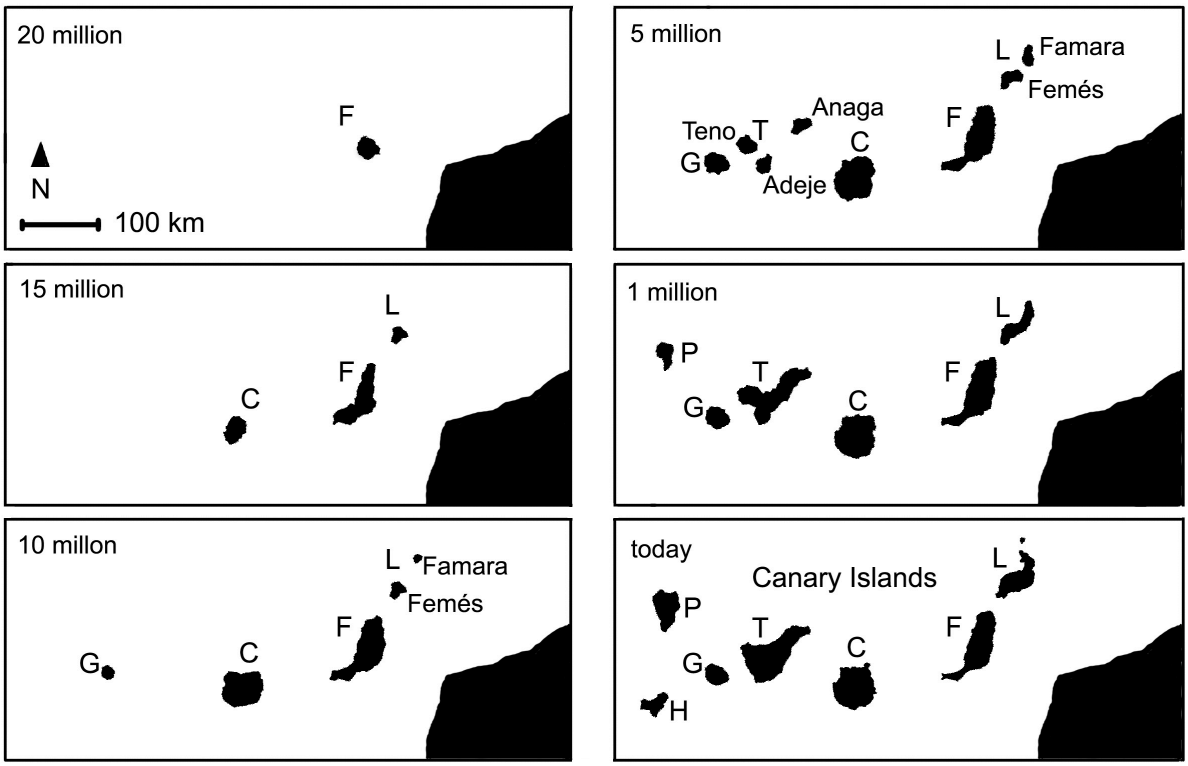

Figure 1: *History of the volcanic evolution of the Canarian Archipelago: L=Lanzarote, F=Fuerteventura, C=Gran Canaria, T=Tenerife, P=La Palma, G=La Gomera, H=El Hierro (Modified after Marrero and Francisco-Ortega 2002).*

The islands have always been separated from the African mainland by a trench which has a recent depth of at least 1,500 m. Sea level changes driven by glacial/interglacial cycles of the Pleistocene were responded by a fluctuating distance to Africa ranging from 60 km (glacial period with low sea-level) to 95 km today (Gracía-Talavera 1999; Fernandez-Palacios and Whittaker 2008).

The seven main islands differ noticeable in size, altitude, and age. Tenerife is seven times larger than El Hierro and its highest elevation, El Teide (3,718 m), is by far higher than for instance on Lanzarote (670 m). These topographic differences are reflected by climatic gradients within and between islands. On Tenerife, mean annual temperature at the highest meteorological station (Cañadas-Pico Teide; 3,530m asl) is 3.5°C, while the lowest station (Anaga-San Andrés; 20m asl), records 20.6°C mean annual temperature (DEL-ARCO et al. 2006). Because of the predominant north-eastern trade winds, precipitation varies especially between north-eastern and south-west facing slopes. On Tenerife, the station with the lowest annual precipitation (Guía de Isora-Alcalà Chiquita; 70m asl) is located on the south-western coast in the rain shadow of El Teide. It only has 47.4mm of annual precipitation. Highest precipitation is recorded on the Esperanza Ridge (Matanza-Lagunetas; 1,400m asl) on the north-eastern part of the island with 928mm of annual precipitation (DEL-ARCO et al. 2006). Despite the indicated spatial variations and regional climate distinctions, in general the Canary Islands are characterised by an even-tempered, subtropical climate that is balanced by the sea, constant trade winds and ocean currents.

3. Methods

This study analyses presence/absence data for *Arthropoda* (7044 species), *Spermatophyta* (1962 species), *Fungi* (1713 species), *Lichenes* (1262 species), *Bryophyta* (474 species), terrestrial *Mollusca* (240 species), *Chordata* (137 species), *Pteridophyta* (63 species), *Annelida* (61 species) and *Nematoda* (31 species) for the seven Canarian main islands. The data were obtained from

Izquierdo *et al*. (2004). Subspecies were excluded. Altogether the dataset contains 12,997 species of which 3,663 are endemic to the Canary Islands.

In a first survey, species richness and the percentage of island endemic species (pSIE) for the different species groups were analysed. Variables used to describe island characteristics are listed in table 1 and table 2.

To identify the amount of total variation explained by ecological, spatial and historic variables, a hierarchical partitioning was conducted. Hierarchical partitioning was developed to estimate the joint and independent contribution of correlated predictor variables. The independent contribution is the part of variance that only one single predictor can explain, while the joint contribution can be explained by more than one predictor. Hierarchical partitioning computes the independent contribution by comparing the goodness-of-fit of all possible models with and without a predictor variable (for more details see Chevan and Sutherland 1991; Mac Nally 2002). The purpose of hierarchical partitioning is not to calculate a predictive model, but to generate a detailed basis for inferring causality in multivariate regression settings (Watson and Peterson 1999). Heikkinen et al. (2005) suggest hierarchical partitioning, as it contributes to a better understanding of predictive variables in ecological studies.

Hierarchical partitioning was conducted using linear regression and R^2 as the goodness-of-fit measure implemented in the package "hier.part" version 1.0-3 (Walsh and Mac Nally 2008) within the statistical program R (R Development Core Team 2008).

As the algorithm is only capable to consider nine variables, the variables with highest explained variance were identified in a preliminary investigation. Hierarchical partitioning was applied on nine coincidentally chosen variables. Then, these variables were weighted according to their explained variance. This procedure was repeated 500 times. Weighting scores for each variable were summed up and those nine variables with the highest cumulative scores were chosen for the final hierarchical partitioning.

As hierarchical partitioning does not provide significance values, a separate linear regression model was calculated for each predictor with the dependent variable (linear regression and R^2 as the goodness-of-fit measure). Significance ($p < 0.05$) was tested using F-test as implemented in function "lm" within the statistical program R.

In a further analysis, the explanatory power for the similarity in species composition was assessed. For the survey of similarity between the Canary Islands, the Simpson Index was chosen. This index is independent of richness (Koleff et al. 2003; Baselga 2007) and is widely used. Similarity indices were calculated by using R-package "simba" version 0.2-5 (Jurasinski 2007).

The geographical distance between the islands and the calculated Euclidean distance of selected variables (listed in table 1) were implemented as predictive variables for the biogeographical analysis. As explained above, the detection of explanatory power was performed by using hierarchical partitioning.

Significance tests for linear relations between distance matrices have to account for the problem of pseudoreplication. One solution is to apply permutation tests. Here, a Mantel-test was performed using R-package "ecodist" version 1.1.4 (Goslee and Urban 2007).

Finally, the percentage of single island endemics (pSIE) was investigated in detail. The connection to species diversity and other already mentioned variables were analysed. Analyses were restricted to *Arthropoda* (SIE n=1,534), *Spermatophyta* (SIE n=294), *Fungi* (SIE n=99) and *Mollusca* (SIE n=173). *Lichenes* (SIE n=14), *Bryophyta* (SIE n=4), *Chordata* (SIE n=6), *Pteridophyta* (SIE n=1), *Annelida* (SIE n=0) and *Nematoda* (SIE n=1) were not taken into considerations due to the small number of SIE.

Table 1: *References and descriptions for the variables used for the analyses. "Island circumference" as well as "inclination under 20%" (not listed here) were not included in later calculations, as they are strongly correlated with "area 2D" and "inclination", respectively.*

Variable name	Description	Reference
Area 2D	Island area in a two dimensional projection	Instituto Nacional de Estadistica (2005)
Area 3D	Three dimensional island area calculated from a digital elevation model.	SRTM-data performed in ENVI 4.0
Elevation	Island elevation	Instituto Nacional de Estadistica (2005)
Time	Represents the time that was available for species immigration and evolution on an island. As suggested by Whittaker et al. (2007, 2008), an age of 8 million years was chosen for Tenerife, as at that time the lava domes that would later form the island exceeded see level. Due to the sterilising volcanic eruption 3.5 million years ago, this time span was chosen for Gran Canaria.	Whittaker et al. (2007, 2008)
Island age	The maximum age of the island.	In DEL ARCO et al. (1996) modified with new records reported in Whittaker et al. (2007, 2008).
Population	Human population on the island.	Instituto Nacional de Estadistica (2005)
Distance to Africa	The nearest geographical distance to mainland Africa.	Google Earth
Next island	The shortest distance to the next island measured from coast to coast.	Google Earth
Mean distance	The mean of an island's distance to all other islands. This mean island distance is the higher the closer to the edge of the archipelago an island is situated	Google Earth
Connectivity	A measurement for travelling possibilities between the islands. It represents the maximum number of ferry and aerial connections that could be found per day and island.	All available net sources that could be found within a two-hour survey.
Soil	The number of illustrated main classes in the map.	Instituto Geográfico Nacional (1994)
Geology	The number of illustrated main classes on the geological map.	Geological map assessed from GRAFCAN – Sistema de información territorial, Gobierno de Canarias
Mean precipitation	Mean precipitation on the island.	FERNANDO-PULLÉ (1976)
Max. precipitation	Precipitation of the meteorological station with highest mean precipitation on the island.	Meteorological data were taken from DEL ARCO et al. (1996), DEL ARCO et al. (1999), REYES-BETANCORT et al. (2001), DEL ARCO et al. (2002), DEL ARCO et al. (2006), DEL ARCO et al. (2008) based on RODRÍGUEZ-DELGADO et al. (2005), DEL ARCO et al. (2009), www.climatedata.eu (02/2010) and www.globalbioclimatics.org (02/2010).
Min. precipitation	Precipitation of the meteorological station with lowest mean precipitation on the island.	See "max. precipitation"
Precipitation range	The range between maximal and minimal precipitation	See "max. precipitation"
Max. temperature	Temperature of the meteorological station with highest mean temperature on the island.	See "max. precipitation"

Min. temperature	Temperature of the meteorological station with lowest mean temperature on the island.	See "max. precipitation"
Temperature range	The range between maximal and minimal temperature.	See "max. precipitation"
Forest cover	The percentage of island area that is covered by forest	Forest management plan published by the Canarian ministry (Consejería de Política Territorial y Medio Ambiente Gobierno de Canarias, 2000)
inclination	Mean inclination of the island calculated from a digital elevation model.	SRTM-data performed in ENVI 4.0

4. Results

Altitude was attributed with the highest explanatory power for species richness (figure 2). It explains the largest proportion of variance for most species groups (R^2 between 0.55 and 0.90). Other variables such as the temperature range, the minimum temperature, precipitation range, the human population, the mean distance to the other islands, human connectivity and the number of soil types also have a high explanatory power. Due to the high inter-correlations among these variables, a precise differentiation between them seemed neither possible nor reasonable. Good predictor variables for pSIE are human population size, mean distance to the other islands, minimum temperature and elevation (figure 3). Similarity in species composition is best reflected by geographical distance, difference in the precipitation parameters and distance to mainland Africa (figure 4). Furthermore, the differences in inclination were a good predictor for similarity. Median values for similarity in species composition vary between 0.9 (for *Annelida*) and 0.4 (*Mollusca*) (figure 5). Incomplete records in species groups that are difficult to detect or to determine, such as *Fungi* and *Lichenes,* could be the reason for low values and a high variance of similarity. Different taxa might erroneously be assumed to be identical. Some species are distinct but can not be discriminated visually. Morphological variability may lead to the description of separate species, which are in fact just varieties. Such problems are likely to occur also in *Annelida* and *Nematoda*. However, the high values of variance are probably related rather to the low number of species in these groups. The species group "*Arthropoda*" is rich in species and ecologically very heterogeneous. Hence, similarity values are close to the overall mean. For *Chordata,* the high similarity of species composition between the islands reflects the large percentage of birds with high migratory ability. Strong distance decay was identified for most species groups (figure 6). The explanatory power of the distance-decay relation is best for *Chordata*.

Table 2: *Variables used for the analyses.*

Variable name	El Hierro	La Palma	La Gomera	Tenerife	Gran Canaria	Fuerteven-tura	Lanzarote
Area 2D [km^2]	269	708	370	2034	1560	1660	846
Area 3D [km^2]	308	777	413	2127	1645	1675	823
Elevation [m a.s.l.]	1501	2423	1487	3718	1949	807	671
Time [million year]	1.1	1.5	12.0	8.0	3.5	16.0	20.0
Island age [million year]	1.1	1.6	12.0	8.0	13.9	16.1	20.0
Population [thousand]	11	86	22	853	807	90	127
Distance to Africa [km]	382	416	333	287	196	96	127
Next island [km]	61	58	27	27	61	11	11
Mean distance [km]	197	184	141	112	140	195	252
Connectivity [number of connections]	13	29	9	76	71	42	34
Soil [number of main types]	3	7	4	7	5	2	3
Geology [number of main types]	9	10	11	27	21	22	11
Mean precipitation [mm]	426	586	410	420	325	147	135
Precipitation range [mm]	718	1123	609	881	842	141	122
max. precipitation [mm]	827	1295	758	928	987	246	218
min. precipitation [mm]	109	172	149	47	145	105	96
Temperature range [°C]	9.5	11.7	8.2	18.6	8.9	2.5	3
max. temperature [°C]	22.2	21.3	20.8	22.1	21.5	20.4	21
min. temperature [°C]	12.7	9.6	12.6	3.5	12.6	17.9	18
Forest cover [%]	24	45	25	24	10	0	0
Inclination [%]	27	33	39	23	28	13	10
Species richness [-]	2879	5189	4509	9008	5987	2839	2590
Number of Arthropoda [-]	1310	2655	2181	4777	3151	1620	1338
Number of Spermatophyta [-]	619	836	848	1383	1256	701	673
Number of Fungi [-]	206	917	502	1073	477	31	60
Number of Lichenes [-]	287	529	531	878	302	76	165
Number of Bryophyta [-]	189	318	278	408	293	122	109
Number of Mollusca [-]	33	55	62	103	69	30	35
Number of Chordata [-]	63	65	68	104	95	68	62
Number of Pteridophyta [-]	33	41	41	53	47	16	14
Number of Annelida [-]	11	20	21	57	24	6	3
Number of Nematoda [-]	8	9	9	24	9	3	8
Endemic species [-]	757	1128	1181	2228	1509	623	561
pSIE [%]	5	5	7	10	9	5	4

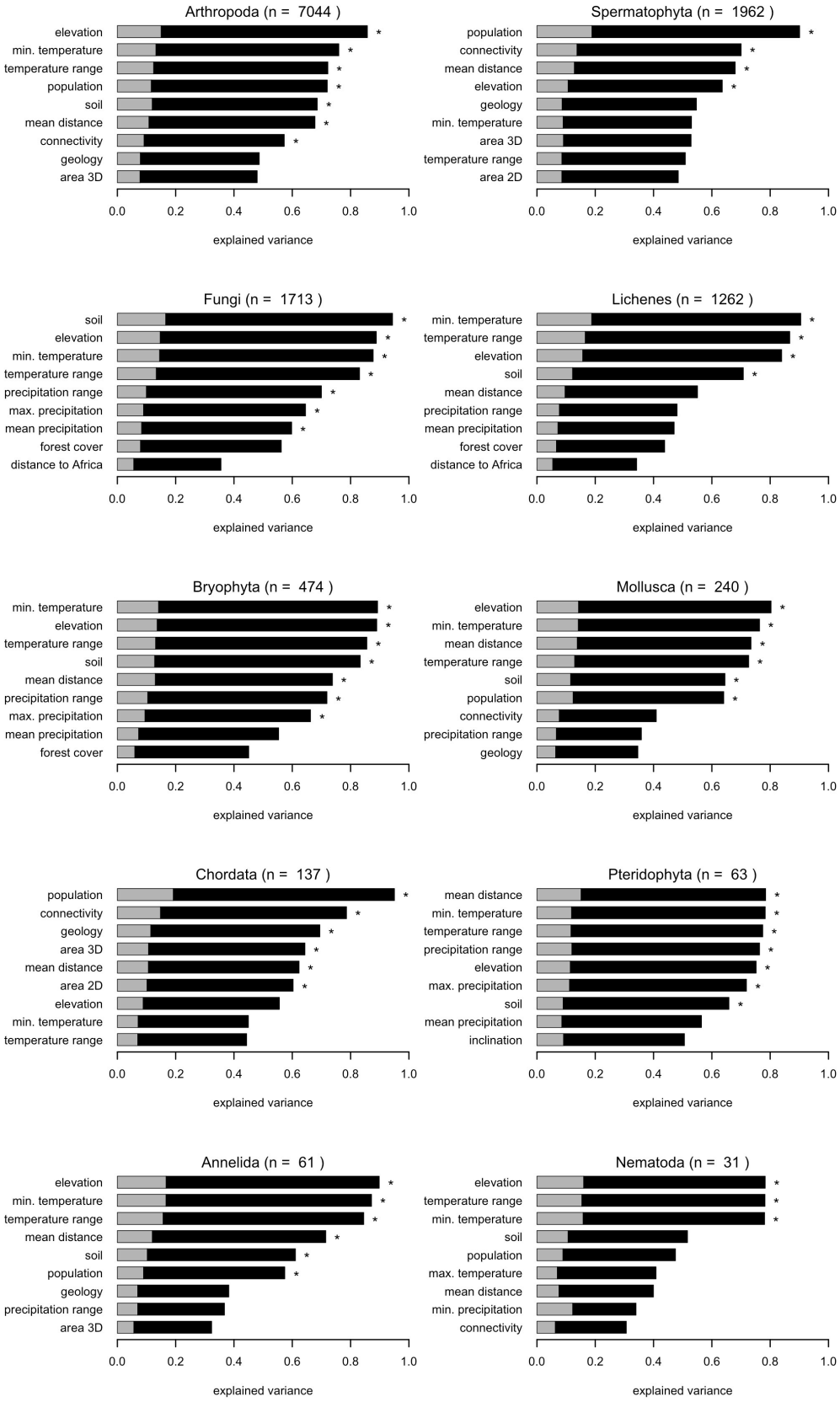

Figure 2: *The number of species was analysed using hierarchical partitioning. The grey parts of the bars illustrate the amount of variance that a variable can explain independently, black parts show the amount of variance that a variable can explain together with other variables. Significance ($p < 0.05$) is indicated by a star behind the bar.*

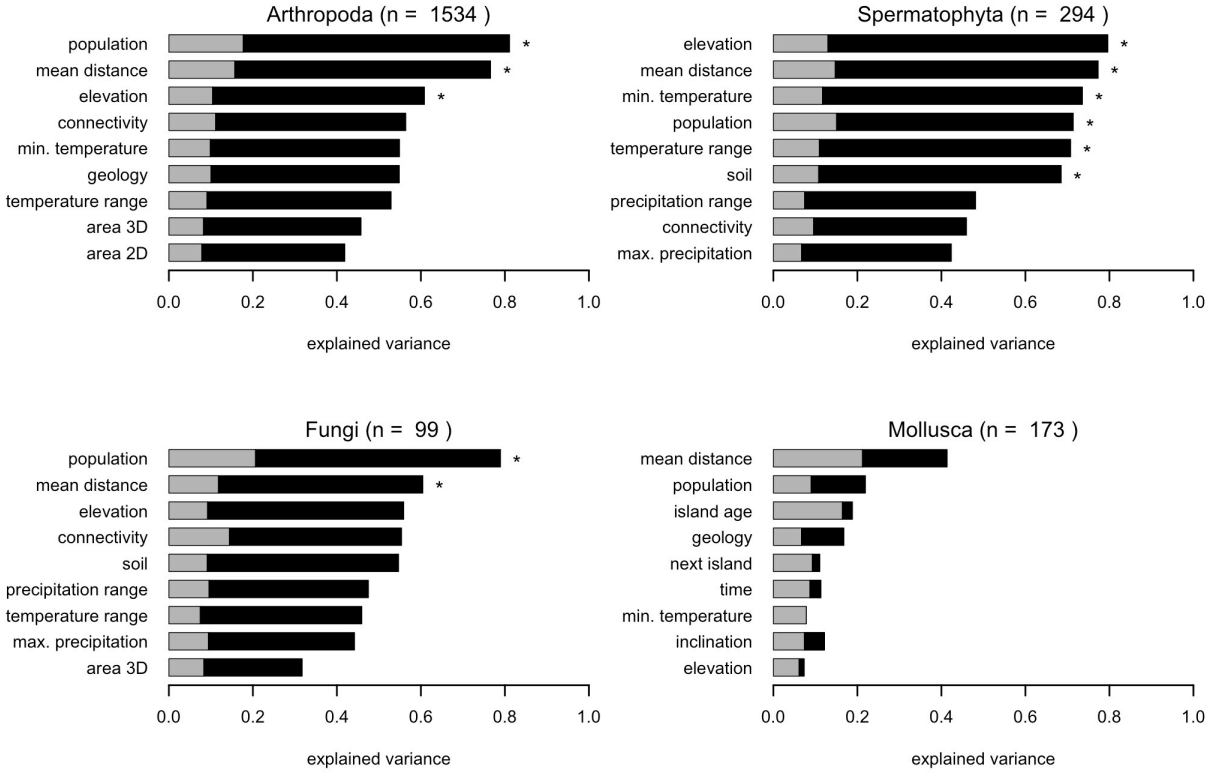

Figure 3: *The percentage of single island endemic species was analysed using hierarchical partitioning. The grey parts of the bars illustrate the amount of variance that a variable can explain independently, black parts show the amount of variance that a variable can explain together with other variables. Significance ($p < 0.05$) is indicated by a star behind the bar.*

5. Discussion

5.1. Variables correlated with the species richness pattern (H1):

Island elevation was identified to be most suitable for describing species richness patterns on the Canary Islands (figure 2). This is consistent with the findings of Fernández-Palacios and Andersson (2000). Elevation summarises a variety of habitat characteristics. Together with predominant wind patterns, elevation is responsible for a manifold mesoclimate. Especially, higher elevations cause pronounced windward and leeward effects. Fernández-Palacios and Andersson (2000) find elevation to be strongly correlated (95%) with habitat diversity on Macaronesian Islands. For the Canary Islands, elevation might substitute area as the variable summarising ecological conditions and carrying capacity. This is consistent with other oceanic island archipelagos (e.g. Hamilton et al. 1963), especially if they are of volcanic origin (like Hawaii; Price 2004). However, a high explanatory power of elevation for area or species richness is not a global phenomenon (Kreft et al. 2008).

An increase of island species diversity with island elevation must not necessarily be caused by habitat diversity. Schoener et al. (2001) show elevation to be a key variable for species survival during catastrophic events (e.g. storm floods, fire). In addition to advantages during short-term events, elevation gradients also facilitate populations persistence and survival during long-term environmental fluctuations such as cold stages.

Besides altitude, variables like “precipitation range”, “minimum temperature”, “medium distance to other islands” and “number of soil types” are suitable variables to describe the distribution pattern. These variables can be understood as the integral of abiotic conditions on the islands. Elevation represents topography. “Number of soil types”, “minimum temperature” and “precipitation range” are defining living conditions for biota. These variables could also be seen to represent mechanisms that define the islands’ ecological niches and carrying capacity.

Consequently, even a higher rate of species immigration will not necessarily result in a much larger number of overall species. Hypothesis 1 could be proved: It is not primarily the recent distance to mainland Africa that influences species abundance on the Canary Islands. Yet the influence of distance cannot be neglected, as indicated by the effects of "mean [island] distance". The identified effect illustrates that islands located in the centre of the archipelago host more species than those at the borders. As two islands with comparably high elevations are located in the centre of the archipelago (Gran Canaria, Tenerife), one could dismiss this effect as a coincidental correlation. However, the pattern we found could also be interpreted as an indication for the importance of species exchange among the islands. This would mean that within archipelagos, immigration from neighbouring islands is more important for species richness than immigration from the mainland. This argumentation would support the results of Sanmartín et al. (2008) who applied a Bayesian modelling approach on the Canary Islands and found the inter-island dispersal within the archipelago to be more important for the explanation of diversification within lineages than dispersal between the continent and the islands.

5.2. pSIE as an indicator for speciation:

pSIE was introduced as a indicator for speciation on island archipelagos by Emerson and Kolm 2005 (see also Whittaker et al. 2007). As pSIE and species number show colinearity for the Canary Islands, it is not surprising that again variables correlated with elevation have the highest explanatory power. However, while elevation is among the best variables that explain pSIE, it is not the overall best (compare figure 3). Emerson and Kolm (2005) identified a correlation between species richness and pSIE for the Canary Islands. They suggested that species richness promotes speciation. In that study, species richness was, besides elevation and area, the most adequate variable for the explanation of distribution patterns of *Spermatophyta* and *Arthropoda*. We show that there are more variables representing either ecological or distance related factors that could explain most variance of the pattern. Therefore, the identified linkage between species number and pSIE could be driven by hidden underlying processes. Whittaker et al. (2007; 2008) suggest that a higher complexity of an island will enable more colonists to find suitable habitats to establish. This will further on intensify the adaptive radiation of already established species. With time, this will deepen the genetic gap between populations on different islands. It is assumed that speciation is stimulated by the availability of more ecological niches. These are considered to be especially diverse on young and topographically heterogeneous islands. Heaney (2000) points to the fact that immigration and speciation exclude each other to a certain extent. Both are related to distance from a species source region.

These linkages between speciation, ecological complexity (Whittaker et al. 2007; 2008) and the distance to species source region (Heaney 2000; Lomolino 2000a), together with the results presented here, suggest an alternative explanation for the correlation between species richness and pSIE. There might be an isolation gradient with altitude within an island. High elevation ecosystems on the mainland (possible source regions) are more probably to be found in the inland, far from to the coastline. Consequently, high elevation ecosystems on islands are farther away from potential species source regions on the mainland than this is the case for low elevation ecosystems. Species that have adapted to high elevation ecosystems have to cross a larger distance and a larger ecological gradient to reach a suitable habitat than low elevation species. The high elevation ecosystems are genetically more isolated (low immigration rate) and will thus have a higher rate of speciation. In the case of the Canary Islands, ecosystems with comparable altitude as El Teide (Tenerife) can again be found in the High Atlas Mountains. In future research, investigations on species distribution and speciation on oceanic islands should not only focus on island level, but rather also differentiate zonal ecosystems on these islands.

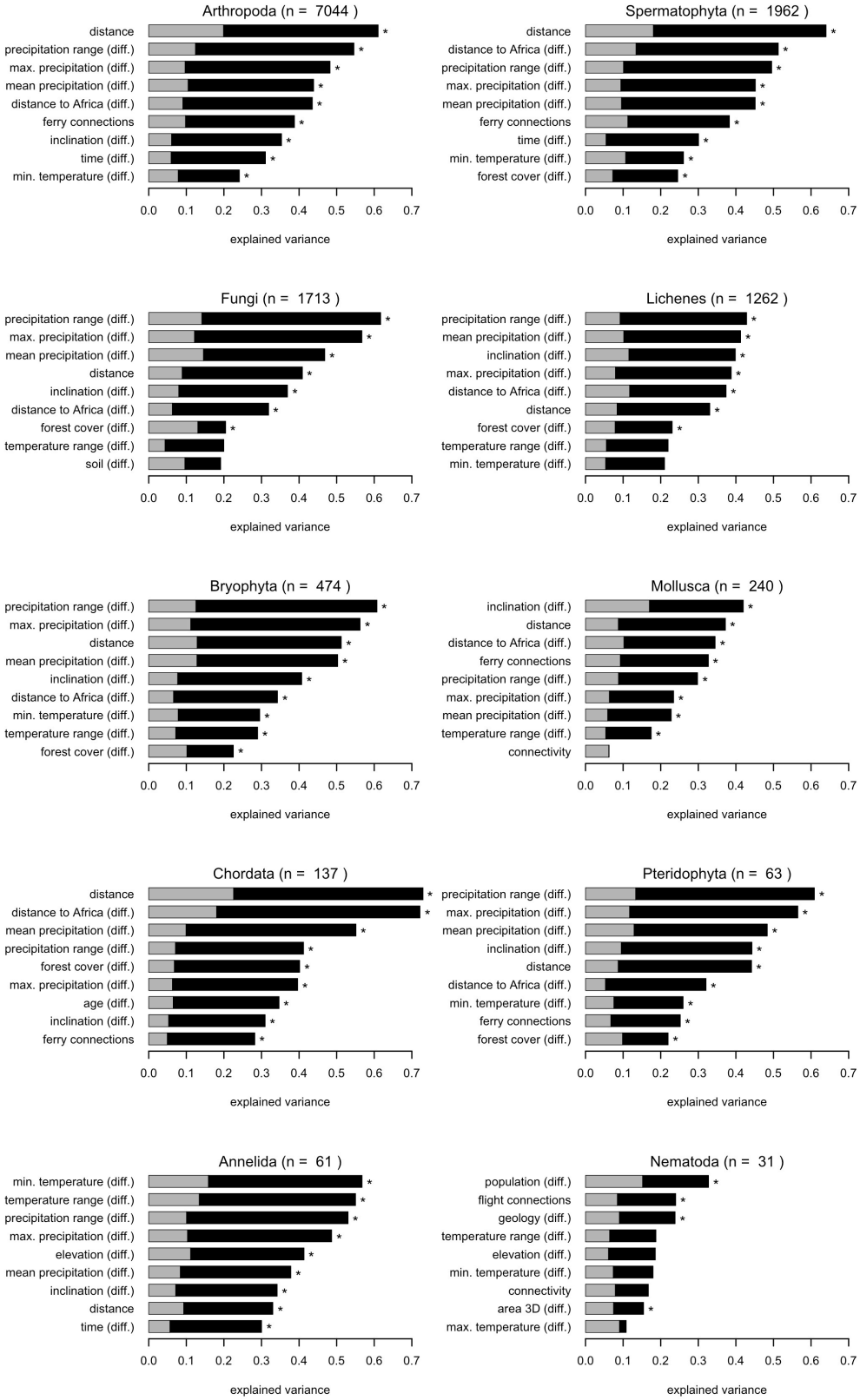

Figure 4: *Beta diversity was analysed using hierarchical partitioning. The grey parts of the bars illustrate the amount of variance that a variable can explain independently, black parts show the amount of variance a variable can explain together with the other variables. Note that the Euclidian distance of the variables listed in table 1 was used for the analyses of similarity. Significance ($p < 0.05$) is indicated by a star behind the bar. The sum of all single island endemic species of a group on the Canary Islands is indicated in brackets.*

5.3. Similarity in species composition (H2)

On the Canary Islands, similarity in species composition is strongly influenced by geographic distance (falsifying hypothesis 2). The high explanatory power of the distance between the islands and the differences in the distance to mainland Africa for similarity values confirms the rule of "distance-decay" (Nekola and White 1999; Baselga 2007). Contributing mechanisms are the decline in the exchange of organisms, an increasing dissimilarity in abiotic and biotic circumstances and distance itself (Nekola and White 1999).

Hints on the migratory and dispersal ability within species groups can be obtained by using the explanatory power of distance (figure 6) together with the median values of similarity in species composition (figure 5). Wind dispersal of diaspores between islands may explain the high values in similarity within plants. The slight increase in mean similarity from *Spermatophyta* over *Bryophyta* to *Pteridophyta* indicates increased colonisation success, probably due to the smaller size of spores and thus a larger importance of wind dispersal in the later groups. As nearly all other ways of dispersal are more constrained by distance than wind dispersal, the decrease in explanatory power by distance (figure 6) from *Spermatophyta* to *Pteridophyta* supports this hypothesis. However, *Fungi,* which can be dispersed via microscopic spores as well, were expected to have higher similarity values. One explanation may be the close dependence on a specific environment or host organism (e.g. *Spermatophyta*). Many fungi can only establish themselves if taxa of an other group of organisms are already there. Low median values in similarity for *Mollusca* represent the low dispersal ability of this group. A low explanatory power of the distance-decay relationship could indicate that immigration is more dependent on stochastic events (like birds transporting eggs from one island to the next) than on migration. High similarity values together with a strong distance-decay for *Chordata* might reflect that some species within the group (such as birds) have colonised all islands, while others (such as amphibians) have limited capacity to cross the ocean.

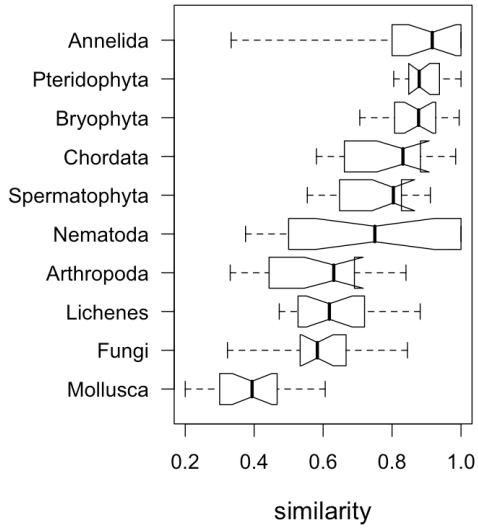

Figure 5: *Similarity values for pairs of islands differentiated for species groups. Dark lines in the box-and-whisker plots represent the median values, boxes indicate quartiles and whiskers data extremes.*

5.4. Changes in ecological settings

Historic changes in the ecological settings of islands (e.g. pedogenesis, erosion, tectonic activity) and modifications of the distances between them (e.g. temporarily available stepping stones, sea level rise) contribute to the explanation of species distribution and speciation on archipelagos. The apparent problem is the difficulty, if not impossibility, to measure or capture historical conditions. As we can not ignore the importance of time and age, proxies have to be included in analyses. In this paper, island age has been corrected for volcanic events that have sterilised the whole surface of an island. 3.5 million years ago, the island of Gran Canaria was sterilised by the eruption of the Roque Nublo. Only two small hideaways remained after the catastrophe (Francisco-Ortega et al. 1996).

Eustatic sea level fluctuations during the Pleistocene (more than 100m) alternately doubled and halved the area of the islands from 14,000 km^2 during the glacial period to 7,500 km^2 during the interglacial (García-Talavera 1999). During the climax of the last glaciation, the relative elevation of the islands was about 130 m higher than the present elevation. Fuerteventura and Lanzarote were connected, forming the island of Mahan with a surface of 5,000 km^2. The distance to the African mainland diminished from today's 100 km to roughly 60 km. In addition, small sea mounds exceeded the sea level as islands and formed ''stepping stones'' between the

Canary Islands, Madeira and the Iberian Peninsula (Whittaker and Fernández-Palacios 2007). This might have promoted species interchange.

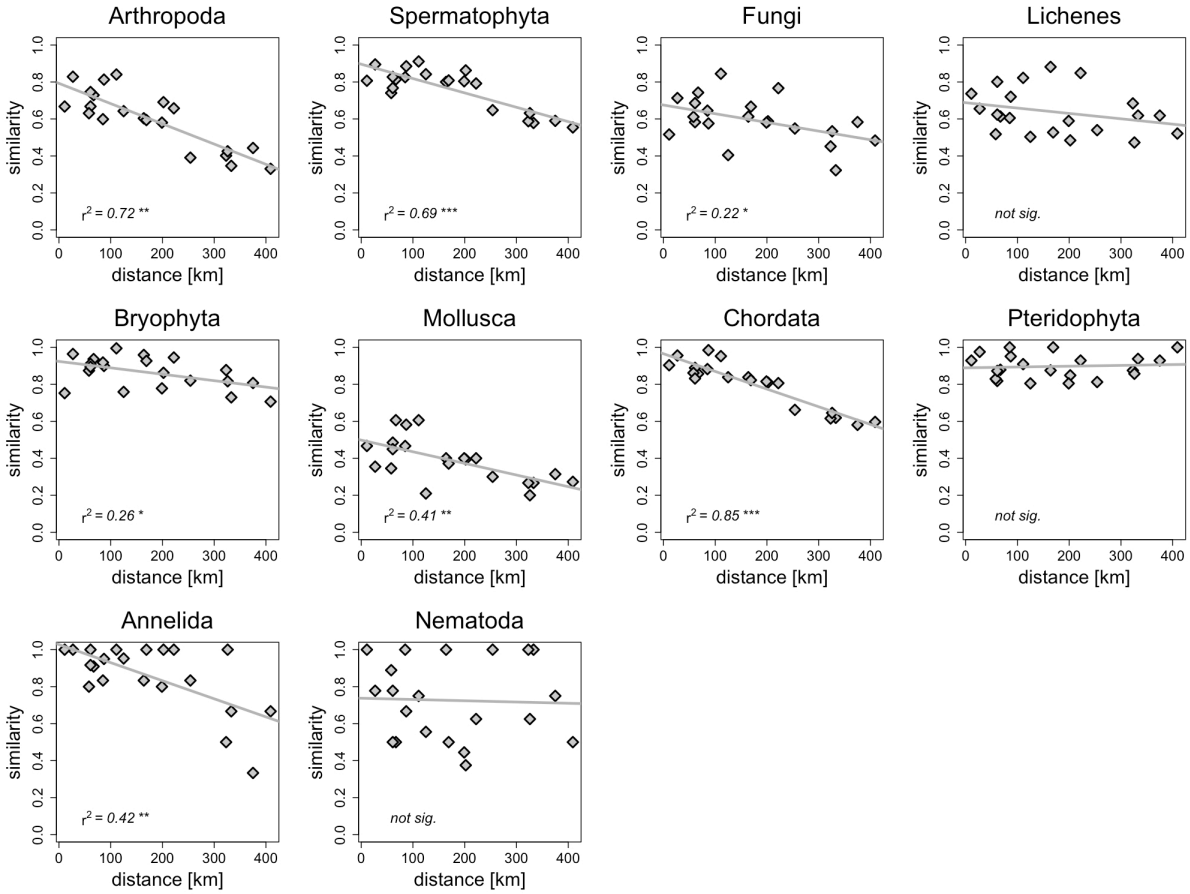

Figure 6: *Relationship between similarity of species composition and geographical distance between the islands. Each dot marks one of a total of 21 inter-insular relationships.*

The evolution of island biodiversity does not only reflect the continuous and long-term development of relief and environment. Single short-term events such as volcanic eruptions and large landslides have strong impacts. By eradicating a large percentage of a certain population, such events might contribute to a narrowing of the genetic pool (Moya et al. 2004). A diminishing population can suffer from inbreeding depression. The genetic depletion can lead through a "bottle neck". After this an increasing population size cannot re-establish the previous genetic diversity and ecological range of the surviving species. Due to limitations in access and measurement, extreme events have been neglected in ecology for a long time. In face of climatic changes, there is increasing attention on disturbances and extremes (Jentsch and Beierkuhnlein 2008). We expect that this perspective will be even more important when evaluating the future development of island floras and faunas.

6. Conclusions

Our results support a strong contribution of ecological complexity to the pattern of species richness. In contrast to other cases (Lomolino 2000b; Tjorve 2003; Triantis et al. 2003), on the Canary Islands elevation is shown to be a more suitable variable than island area to detect complexity and diversity.

Especially on islands with high elevations, distance from high elevation habitats to comparable sites on other islands or on the mainland might vary strongly. High altitude ecosystems on the continent, which are potential sources for species immigration on islands, might be far away from the coast in the inland. In the case of the alpine communities of the Canary Islands, the

nearest neighbours are found in the Atlas Mountains in Morocco. The distance an immigrating species has to overcome affects the driving processes of island biodiversity like immigration or speciation. However, distance and mechanisms are linked to the "ecological" distance between potential habitats and not to the mere geographic distance between islands and a continent. We therefore suggest to focus further research on the ecosystem scale, rather than the island scale. An appropriate approach is to work with elevation zones or with specific ecological settings.

Acknowledgements
We wish to thank Julian Zeidler and Reinhold Stahlmann for their support.

References

Anguita, F.; Márquez, A.; Castineiras, P. and Hernàn, F. (2002): Los volcanes de Canarias. Guía geológica e itinerarios. Alcorón (Madrid).

Baselga, A. (2007): Disentagling distance decay of similarity from richness gradients: response to Soininen et al. 2007. In: Ecography 30, 838–841.

Beierkuhnlein, C. (1998): Biodiversität und Raum. In: Die Erde 128, 81-101.

Beierkuhnlein, C. (2007): Biogeographie. Die räumliche Organisation des Lebens in einer sich verändernden Welt. Stuttgart.

Brown, J. H. and Kodric-Brown, A. (1977): Turnover rates in insular biogeography. Effects of immigration on extinction. In: Ecology 58, 445–449.

Brown, J. H. and Lomolino, M. V. (2000): Concluding remarks: historical perspective and the future of island biogeography theory. In: Global Ecol. Biogeogr. 9, 87–92.

Carroll, S. P.; Hendry, A. P.; Reznick, D. N. and Fox, C. W. (2007): Evolution on ecological time-scales. In: Funct. Ecol. 21, 387–393.

Chevan, A. and Sutherland, M. (1991): Hierarchical partitioning. In: Am. Stat. 45, 90–96.

Connor, E. F. and Mc Coy, E. D. (1979): Statistics and biology of the species-area relationship. In: Am. Nat. 113, 791–833.

Consejería de Política Territorial y Medio Ambiente Gobierno de Canarias (2000): Plan Forestal de Canarias.

Dapporto, L. and Dennis, R. L. H. (2008): Species richness, rarity and endemicity on Italian offshore islands: Complementary signals from island-focused and species-focused analyses. In: J. Biogeogr. 35, 664–674.

Del Arco, M.; Acebes, J. R. and Pérez-De-Paz, P. L. (1996): Bioclimatology and climatophilous vegetation of the Island of Hierro. In: Phytocoenologia 26, 445–479.

Del Arco, M.; Acebes, J. R.; Pérez-De-Paz , P. L. and Marrero, M. C. (1999): Bioclimatology and climatophilous vegetation of Hierro (part 2) and La Palma (Canary Islands). In: Phytocoenologia 29, 253–290.

Del Arco, M.; Salas, M.; Acebes, J. R.; Marrero, M. C.; Reyes-Betancort, J. A. and Pérez De Paz, P. L. (2002): Bioclimatology and climatophilous vegetation of Gran Canaria (Canary Islands). In: Ann. Bot. Fenn. 39, 15–41.

Del Arco, M.; Pérez De Paz, P. L.; Acebes, J. R.; González-Mancebo, J. M.; Reyes-Betancort, J. A.; Bermejo, J. A.; De Armas, S. and González-González, R. (2006): Bioclimatology and climatophilous vegetation of Tenerife (Canary Islands). In: Ann. Bot. Fenn. 43, 167–192.

Del Arco. M. (2008): La flora y la vegetación canaria ante el cambio climático actual. In: Afonso-Carrillo, J. (ed.). Naturaleza amenazada por los cambios en el clima. Actas III Semana Científica Telesforo Bravo, Instituto de Estudios Hispánicos de Canarias. Puerto de la Cruz, Tenerife, 105–140

Del Arco, M.; Rodríguez-Delgado, O.; Acebes, J.R.; García-Gallo, A.; Pérez De Paz, P.L.; González-Mancebo, J.M.; González-González, R. and Garzón, V. (2009): Bioclimatology and climatophilous vegetation of Gomera (Canary Islands). In: Ann. Bot. Fenn. 46, 161-191.

Duarte, M. C.; Rego, F.; Romeiras, M. M. and Moreira, I. (2008): Plant species richness in the Cape Verde islands – eco-geographical determinants. In: Biodivers. Conserv.17, 453–466.

Emerson, B. C. and Kolm, N. (2005): Species diversity can drive speciation. In: Nature 434, 1015–1017.

Fernández-Palacios, J. M. and Andersson, C. (2000): Geographical determinants of the biological richness in the Macaronesian region. In: Acta Phytogeographica Suecica 85, 41–50.

Fernandez-Palacios, J. M. and Whittaker, R. J. (2008): The Canaries: An important biogeographical meeting place. In: J. Biogeogr. 35, 379–387.

Fernando-Pullé, D. (1976): Climatic characteristics of the Canary Islands. In: Kunkel, E. (ed.): Biogeography and ecology in the Canary Islands. Monographiae Biologicae 30. The Hague.

Francisco-Ortega, J.; Jansen, R. K. and Santos-Guerra, A. (1996): Chloroplast DNA evidence of colonization, adaptive radiation, and hybridization in the evolution of the Macaronesian flora. In: Proc. Natl. Acad. Sci. USA 93, 4085–4090.

Fussmann, G. F.; Loreau, M. and Abrams, P. A. (2007): Eco-evolutionary dynamics of communities and ecosystems. In: Funct. Ecol. 21, 465–477.

García-Talavera, F. (1999): La Macaronesia. Consideraciones geológicas, biogeográficas, y paleoecológicas. In: Fernández Palacio, J.; Bacallado, J. J. and Belmonte, J. A. (eds.): Ecología y cultura en Canarias. Santa Cruz de Tenerife, 39–64.

Goslee, S. C. and Urban, D. L. (2007): The ecodist package for dissimilarity-based analysis of ecological data. In: Journal of Statistical Software 22, 1–19.

Halas, D.; Zamparo, D. and Brooks, D. R. (2005): A historical biogeographical protocol for studying biotic diversification by taxon pulses. In: J. Biogeogr. 32, 249–260.

Hamilton, T. H.; Rubinoff, I.; Bush, G. L. and Barth, R. H. (1963): Species abundance – Natural regulation of insular variation. In: Science 142, 1575–1577.

Hannus, J. J. and von Numers, M. (2008): Vascular plant species richness in relation to habitat diversity and island area in the Finnish Archipelago. In: J. Biogeogr. 35, 1077–1086.

Heaney, L. R. (2000): Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography. In: Global Ecol. Biogeogr. 9, 59–74.

Heaney, L. R. (2007): Is a new paradigm emerging for oceanic island biogeography? In: J. Biogeogr. 34, 753–757.

Heikkinen, R. K.; Luoto, M.; Kuussaari, M. and Pöyry, J. (2005): New insights into butterfly-environment relationships using partitioning methods. In: Proceedings of the Royal Society 272, 2203–2210.

Instituto Geográfico Nacional (1994): Atlas Nacional de España. Ministerio de Obras Públicas, Transportes y Medio Ambiente. Madrid.

Instituto Nacional de Estadistica (2005): Anuario Estadístico de España. Librerías Índice, Madrid.

Izquierdo, I.; Martín, J. L.; Zurita, C. and Arechavaleta, M. (2004): Lista de especies silvestres de Canarias. Hongos, plantas y animales terrestres. Consejería de Médio Ambiente y Ordenación Territorial, Gobierno de Canarias, La Laguna. Santa Cruz de Tenerife, Islas Canarias.

Jentsch, A. and Beierkuhnlein, C. (2008): Research frontiers in climate change: effects of extreme meteorological events on ecosystems. In: CR Geoscience 340, 621-628.

Jurasinski, G. (2007): simba: A collection of functions for similarity calculation of binary data. R-package.

Jurasinski, G.; Retzer, V.; Beierkuhnlein, C. (2009): Inventory, differentiation, and proportional diversity – a consistent terminology for quantifying biodiversity. In: Oecologia 159, 15-26.

Kinnison, M. T. and Hairston, N. G. (2007): Eco-evolutionary conservation biology: Contemporary evolution and the dynamics of persistence. In: Funct. Ecol. 21, 444–454.

Koleff, P.; Gaston, K. J. and Lennon, J. J. (2003): Measuring beta diversity for presence-absence data. In: J. Anim. Ecol. 72, 367–382.

Kreft, H.; Jetz, W.; Mutke, J.; Kier, G. and Barthlott, W. (2008): Global diversity of island floras from a macroecological per- spective. In: Ecol. Lett. 11, 116–127.

Lomolino, M. V. (2000a): A call for a new paradigm of island biogeography. In: Global Ecol. Biogeogr. 9, 1–6.

Lomolino, M. V. (2000b): Ecology's most general, yet protean pattern: the species-area relationship. In: J. Biogeogr. 27, 17–26.

MacArthur, R. H. and Wilson, E. O. (1967): The theory of island biogeography. Princeton.

Mac Nally, R. (2002): Multiple regression and inference in ecology and conservation biology: further comments on identifying important predictor variables. In: Biodiv. Cons. 11 (8), 1397–1401.

Marrero, A. and Francisco-Ortega, J. (2002): Evolución en islas: la metáfora espacio-tiempo-forma. In: Fernández-Palacios, J. M. and Martín Esquivel, J. L. (eds.): Naturaleza de las Islas Canarias. Ecología y conservación. Santa Cruz de Tenerife, 133–140.

McMaster, R. T. (2005): Factors influencing vascular plant diversity on 22 islands off the coast of eastern North America. In: J. Biogeogr. 32, 475–492.

Morrison, L. W. (2002): Determinants of plant species richness on small Bahamian islands. In: J. Biogeogr. 29, 931–941.

Moya, O.; Contreras-Diaz, H. G.; Oromi, P. and Juan, C. (2004): Genetic structure, phylogeography and demography of two ground-beetle species endemic to the Tenerife laurel forest (Canary Islands). In: Mol. Ecol. 13, 3153–3167.

Nekola, J. C. and White, P. S. (1999): The distance decay of similarity in biogeography and ecology. In: J. Biogeogr. 26, 867–878.

Panitsa, M.; Tzanoudakis, D.; Triantis, K. A. and Sfenthourakis, S. (2006): Patterns of species richness on very small islands: the plants of the Aegean archipelago. In: J. Biogeogr. 33, 1223–1234.

Preston, F. W. (1960): Time and space and the variation of species. In: Ecology 41, 611–627.

Price, J. P. (2004): Floristic biogeography of the Hawaiian Islands: influences of area, environment and paleogeography. In: J. Biogeogr. 31, 487–500.

Pulliam, H. R. (1988): Sources, sinks, and population regulation. In: Am. Nat. 132, 652–661.

R Development Core Team (2008): R: A language and environment for statistical computing. Vienna.

Reyes-Betancort, J. A.; Wildpret de la Torre, W.; León-Arencibia, M. C. (2001): The vegetation of Lanzarote (Canary Islands). In: Phytocoenologia 31, 185–247.

Ricklefs, R. E. and Bermingham, E. (2002): The concept of the taxon cycle in biogeography. In: Global Ecol. Biogeogr. 11, 353–361.

Rodríguez Delgado, O.; García-Gallo, A. and Marrero-Gómez, M. V. (2005): El bioclima y la biogeografía. In: Rodríguez Delgado, O. (ed.): Patrimonio natural de la Isla de Fuerteventura. Cabildo de Fuerteventura. Gobierno de Canarias y Centro de la Cultura Popular Canaria. Arafo. Tenerife, 91–100.

Roos, M. C.; Kessler, P. J.; Gradstein, S. R. and Baas, P. (2004): Species diversity and endemism of five major Malesian islands: Diversity-area relationships. In: J. Biogeogr. 31, 1893–1908.

Sanmartin, I.; van der Mark, P. and Ronquist, F. (2008): Inferring dispersal: A Bayesian approach to phylogeny-based island biogeography, with special reference to the Canary Islands. In: J. Biogeogr. 35, 428–449.

Schmitt, T. (1998): Phytodiversität mediterraner Inseln. In: Geographische Rundschau 12, 680–688.

Schoener, T. W.; Spiller, D. A. and Losos, J. B. (2001): Natural restoration of the species-area relation for a lizard after a hurricane. In: Science 294, 1525–1528.

Tjorve, E. (2003): Shapes and functions of species-area curves: A review of possible models. In: J. Biogeogr. 30, 827–835.

Triantis, K. A.; Mylonas, M.; Lika, K. and Vardinoyannis, K. (2003): A model for the species-area-habitat relationship. In: J. Biogeogr. 30, 19–27.

Walsh, C. and Mac Nally, R. (2008): hier.part: Hierarchical Partitioning. R-package.

Watson, D. M. and Peterson, A. T. (1999): Determinants of diversity in a naturally fragmented landscape: humid montane forest avifaunas of Mesoamerica. In: Ecography 22, 582–589.

Whittaker, R. J. (2000): Scale, succession and complexity in island biogeography: are we asking the right questions? In: Global Ecol. Biogeogr. 9, 75–85.

Whittaker, R. J. and Fernández-Palacios, J. M. (2007): Island Biogeography. Ecology, Evolution, and Conservation. Oxford.

Whittaker, R. J.; Triantis, K. A. and Ladle, R. J. (2008): A general dynamic theory of oceanic island biogeography. In: J. Biogeogr. 35, 977–994.

Whittaker, R. J.; Ladle, R. J.; Araujo, M. B.; Fernández-Palacios, J. M.; Delgado, J. D. and Arevalo, J. R. (2007): The island immaturity – speciation pulse model of island evolution: an alternative to the "diversity begets diversity" model. In: Ecography 30, 321–327.

Willerslev, E.; Hansen, A. J.; Nielsen, K. K. and Adsersen, H. (2002): Number of endemic and native plant species in the Galapagos Archipelago in relation to geographical parameters. In: Ecography 25, 109–119.

Williams, C. B. (1964): Patterns in the Balance of Nature and Related Problems in Quantitative Ecology. London.

5. Manuscript 4 - Revaluating the general dynamic theory of oceanic island biogeography

Submitted to Frontiers of Biogeography

Manuel Jonas Steinbauer[1], Klara Dolos[2], Björn Reineking[2], Carl Beierkuhnlein[1]

[1] *Dept. of Biogeography, BayCEER, University of Bayreuth, D-95447 Bayreuth, Germany*
[2] *Biogeographical Modelling, BayCEER, University of Bayreuth, D-95447 Bayreuth, Germany*
Correspondence: Manuel J. Steinbauer, Dept. of Biogeography, BayCEER, University of Bayreuth, D-95447 Bayreuth, Germany. E-mail: Manuel.Steinbauer@uni-bayreuth.de

Abstract
The general dynamic model (GDM) integrates temporal aspects in a conceptual framework of island biogeography. Here we emphasize aspects of the Equilibrium Theory of Island Biogeography that are currently neglected in the GDM. In addition, we correct a significance test and apply mixed effect models to the four diversity indices used in the GDM, i.e. species richness, the number (nSIE) and percentage of single island endemic species (pSIE) and a diversification index (DI), i.e. ratio of nSIE to the genera containing SIE.
The new statistical approach generally confirms previous results derived from the GDM and provides important additional insights. The richness-time relationship is positively skewed. In addition, the hump shaped relation of the diversity indices with time peaks earliest for species richness (2.3 Ma) and the latest for pSIE (9.8 Ma). This indicates that time is needed for speciation. Time thus does not exclusively represent the characteristic ontogeny of an island. Area has a greater effect on species richness and nSIE than on pSIE and DI.
While the GDM is generally accepted and its predictions met, the concept of "carrying capacity" hinders rigorous testing of hypothesis. A hump shaped relation of diversity with time does not need to be associated to a "carrying capacity" (that may not exist). A change in environmental settings associated to the ontogeny of an island can be directly linked to colonisation, extinction and speciation. This enables the development of more precise hypotheses.

Keywords: Diversification, extinction, immigration, island evolution, macroecology, oceanic islands, space-for-time substitution, speciation

Towards a New Synthesis

MacArthur and Wilson's (1963, 1967) equilibrium theory of oceanic island biogeography was seminal in linking ecological processes with observable patterns and geographical features. It was also ground-breaking in providing a first comprehensive theory of island biogeography with testable predictions. Stimulated by this work, island biogeographical theory has proceeded but the need to incorporate further processes (especially speciation) more fully into a general theory of island biogeography has frequently been stressed (e.g. Brown and Lomolino, 2000; Heaney 2000, 2007; Lomolino 2000; Whittaker 2000). Several recent contributions have advanced a new synthesis of a general island biogeographical theory. Among the most important is Whittaker et al.'s (2007, 2008, 2010) general dynamic model of oceanic island biogeography (GDM) being the presently most comprehensive theoretical model for oceanic islands of volcanic origin. The GDM integrates the processes of immigration, speciation and extinction in the temporal frame of the characteristic ontogeny of a volcanic oceanic island. After a volcanic emergence over sea surface, islands are in general transformed by erosion processes making the island first more heterogeneous and then flatter (Whittaker et al. 2007). In addition, for some island systems, the elevation is gradually reduced by subsidence of the underlying tectonic plate, once the volcanic hotspot responsible for its existence has passed by (Fernández-Palacios et al. 2011). The GDM is not an equilibrium theory and neglects interactions among the three fundamental processes of island biogeography. Instead, the GDM suggests that the carrying capacity of an island, which is related to topographic heterogeneity, will increase with an island growing in area and elevation and decline when an island is heading towards submergence. Following this ontogeny of an island, the GDM predicts, beside other hypotheses, a unimodal ("hump-shaped") relation with time (often age of the island) for (1) species richness, (2) the number of single island endemic species (nSIE), (3) the percentage of single island endemic species (pSIE) from overall native richness and a diversification index (DI; expressed by the ratio of nSIE to the number of genera containing SIE) (see Whittaker et al. 2008 for details). While testing these hypotheses Whittaker et al. (2008) find the predicted relations confirmed. However, we think the applied test is statistically not adequate. We follow Bunnefeld and Phillimore (2012) and Hortal (2012) in suggesting the use of mixed effect models as a more appropriate tool for hypotheses testing in island biogeography.

Datasets and Distributions

To test time related aspects like island ontogeny in island biogeographical theories, time series of biotic characteristics e.g. species richness, would be needed. These are not available. Even if data are available for some islands and periods much longer time scales would be needed to explain present distribution of species on islands. Space-for-time substitution is a commonly applied strategy to solve these problems in biogeography. To minimize differences in spatial or ecological settings as well as history, island archipelagos are often taken for tests. The limited number of suitable datasets (i.e. archipelagos) as well as the low number of replicates (islands within defined age classes) strongly restricts the options for statistical tests of island biogeographical theories.

Whittaker et al. (2008) use 14 datasets of different species groups on 5 archipelagos to test the hypotheses of the GDM. Their empirical evaluation of the GDM focuses on predications that connect diversity-related parameters to the ontogeny of volcanic islands. A unimodal relation is predicted for several diversity related variables, which can be expressed by the following formula

$$\text{Dependent} \sim \text{Time} + \text{Time}^2 \quad \textit{; abbreviated as } TT^2 \qquad (1)$$

Whittaker et al. (2008) additionally introduced a correction term for (logarithmic) island area to account for different spatial properties of islands within one archipelago and compared this model to a set of possible alternative models.

Dependent ~ log(Area) + Time + Time^2 *; abbreviated as logATT^2* (2)

In addition, Fattorini (2009) noticed that the species area-relationship is best expressed by a non-linear power function. We identified not only a log-transformed dependent variable but also log-transformed time values to significantly improve model performance and residuals. We thus suggest modifying equation 2 as follows:
log(Dependent) ~ log(Area) + log(Time) + log(Time)^2 *; abbreviated as ATT^2* (3)

Linear regression models are generally tested for significance against a "null model" using F statistics to compare the portions of regression sum of squares. In their original analyses, Whittaker et al. (2008) applied a null model with intercept and regression coefficients all being zero. They thus tested whether the mean of the response variables (nSIE etc.) are significantly different from zero. In contrast the adequate null model is characterized by all regression coefficients being zero but the intercept being the sample mean. This represents two very different null models, and we repeated calculations with the standard null model (results in Appendix S1 in Supporting Information). A significant negative or positive quadratic term in the model formula is an indication for a "hump-shape" or "U-shape" of the relationship, respectively, but the relation could still be asymptotic. The later possibility was excluded by graphical inspection.
Ecological and biogeographical datasets are typically characterized by noise (Simberloff 1980). To separate an existing pattern from noise, large datasets are required. In the case of island archipelagos the small number of replicates sets natural limits to this. Pooling data across archipelagos increases sample size, but observations (island species pools) within an archipelago are in most cases more similar to each other than between comparable islands from other archipelagos. This violates the assumption of independence of observations. Mixed effect models offer an attractive alternative to test theories of island biogeography (Bunnefeld and Phillimore 2012). They incorporate all archipelagos under study into one analysis, thus increasing the statistical power. Regression coefficients are fitted as fixed effects constituting the model of theoretical interest. Variation between archipelagos or species groups can be accounted for by adding random effects on the intercept and/or regression coefficients.
Here we use generalized linear mixed effect models (for equation 1 and 2) with Gaussian error distribution and the identity-link function (for the response variables species richness, number of SIE as well as DI) or binomial error distribution with logit-link function (for the percentage of SIE). Using binomial error distribution for percentage values has the advantage of increasing model performance by including information on the number of cases a percentage value is based on (a value of 5% is more reliable if it is based on 100 individuals than if it is based on 10). Response variables were log (x+c) transformed in case of models with a Gaussian error distribution, to meet the assumption of normally distributed residuals (c = 0 for species richness but for DI and SIE: c= $q1^2$ / q3; where q1 and q3 is the first and third quartile of those observations that unequal zero; Stahel 2002). Log(x+c) transformations bear the problematic issue of slightly changing the true relationship (Millar et al. 2011). However, this very small bias is easier to accept than non-normally distributed residuals. After transformations, visual inspection of model residual plots did not indicate deviations from model assumptions. A random effect for archipelago, species group and island was implemented to the intercept. Significance of a negative quadratic term in the model is an indicator for a hump-shaped relationship. The hump-shape was additionally confirmed by visual inspection. Statistical analyses were performed in R version 2.13.1 (R Development Core Team 2011) using LME4 version 0.999375-40 (Bates et al. 2011).

Results

After applying the suggested null model on the linear regression analyses employed by Whittaker et al. (2008), roughly 50% of the formerly statistically significant models (Whittaker

et al. 2008) lose significance (Table S1 in Supporting Information). But still, in many cases the logATT^2 model (equation 2) remains significant and the model that fits the data best (see Table S1 in Supporting Information and Whittaker et al. 2008 for an overview on alternative models). The general linear and non-linear mixed effect models confirm the ranking of the logATT^2 model (Table 1). However, the *ATT*^{2} (all variables log-transformed) (equation 3) performed better than the logATT^2 model in case of species richness and the number of SIE. Within the ATT^2 models, the effect of log-area [km^2] is more pronounced for nSIE (0.53± 0.05) and species richness (0.40± 0.03) than for pSIE (0.17± 0.03) and DI (0.15± 0.02). The same is true for the logATT^2 models (nSIE 0.53± 0.04; species richness 0.40± 0.02; pSIE 0.16± 0.03; DI 0.15± 0.01). For species richness, the predicted curve of the best model peaks much earlier (2.3 Ma) than for the other diversity indices (SIE: 3.6 Ma), with pSIE peaking ultimately (9.8 Ma; Figure 1a-d). The quadratic term of time (indicating the humped shape of the curve) is most significant for pSIE (<2e-09) followed by richness (<2 e-06) and nSIE (<6 e-04). pSIE is thus presumably the variable that corresponds best to the hypothesis of the GDM.

Table 1: The logATT2 suggested by the GDM performs best for the percentage of endemic species, but the model with an addition log-transformation of time (ATT^2 [log(area) and log(time)]) performs best for species richness and the number of endemic species. The pattern of DI is best explained by a log(area) model. Note that low AIC values indicate a better model performance. Model significance (Pr) was assessed by ANOVA (glme vs. null model). All models are highly significant (p<0.001). Significantly hump shaped relations are indicated by *** for p<0.001 and ** for p<0.01.

	SR (Gaussian)			SIE (Gaussian)		
model	AIC	Pr	Humped shaped	AIC	Pr	Humped shaped
ATT^2	**216**	***	***	**375**	***	
logATT^2	224	***	***	378	***	***
logA	225	***		380	***	
TT^2	307	***	not sig.	437	***	**
A	313	***		445	***	
logT	305	***	***	436	***	
	"pSI" (SR-SIE)/SIE (Binomial)			"DI" (nSIE)/GeneraSIE (Gaussian)		
	AIC	Pr	Humped shaped	AIC	Pr	Humped shaped
ATT^2	514			182	***	**
logATT^2	**497**	***	***	182	***	***
logA	519	***		**178**	***	
TT^2	521	***	***	225	***	**
A	no convergence			232	***	
logT	536	***		221	***	

Perspectives and Challenges

Each island represents a specific development phase (time step) within the idealised ontogeny of volcanic islands. Archipelagos comprising solely old or young islands will thus reflect only a section of the postulated hump-shaped trajectory (Triantis et al. 2011). The real time step an island represents, however, has been cause of debate (Anderson et al. 2009, Whittaker et al. 2007, 2008, 2010). Here, we follow the time estimates used by Whittaker et al. (2008) to favour a comparison of approaches. One of the reasons of uncertainty when estimating the developmental phases of islands is the fact that volcanic activity is often pulsed. In addition, originally separated volcanic island can merge to one composite island as an effect of later

eruptions (e.g. Tenerife; Canary Islands) or sea level changes (during the last glacial maximum Lanzarote and Fuerteventura grew together forming Mahan). Large volcanic events can sterilise whole islands long time after their geological formation (e.g. Gran Canaria). Furthermore, especially instable young oceanic islands can be strongly affected by large landslides. Besides these extreme events, climatic and ecological changes during an island's ontogeny influence topographic heterogeneity. The specific climatic history of an island or archipelago also affects its ecological isolation from climates and ecosystems on a nearby continent (Fernández-Palacios et al. 2011). All these aspects are adding uncertainty to the space-for-time substitution approach. In the light of these considerations, it is striking that the GDM hypothesis appears to be generally applicable.

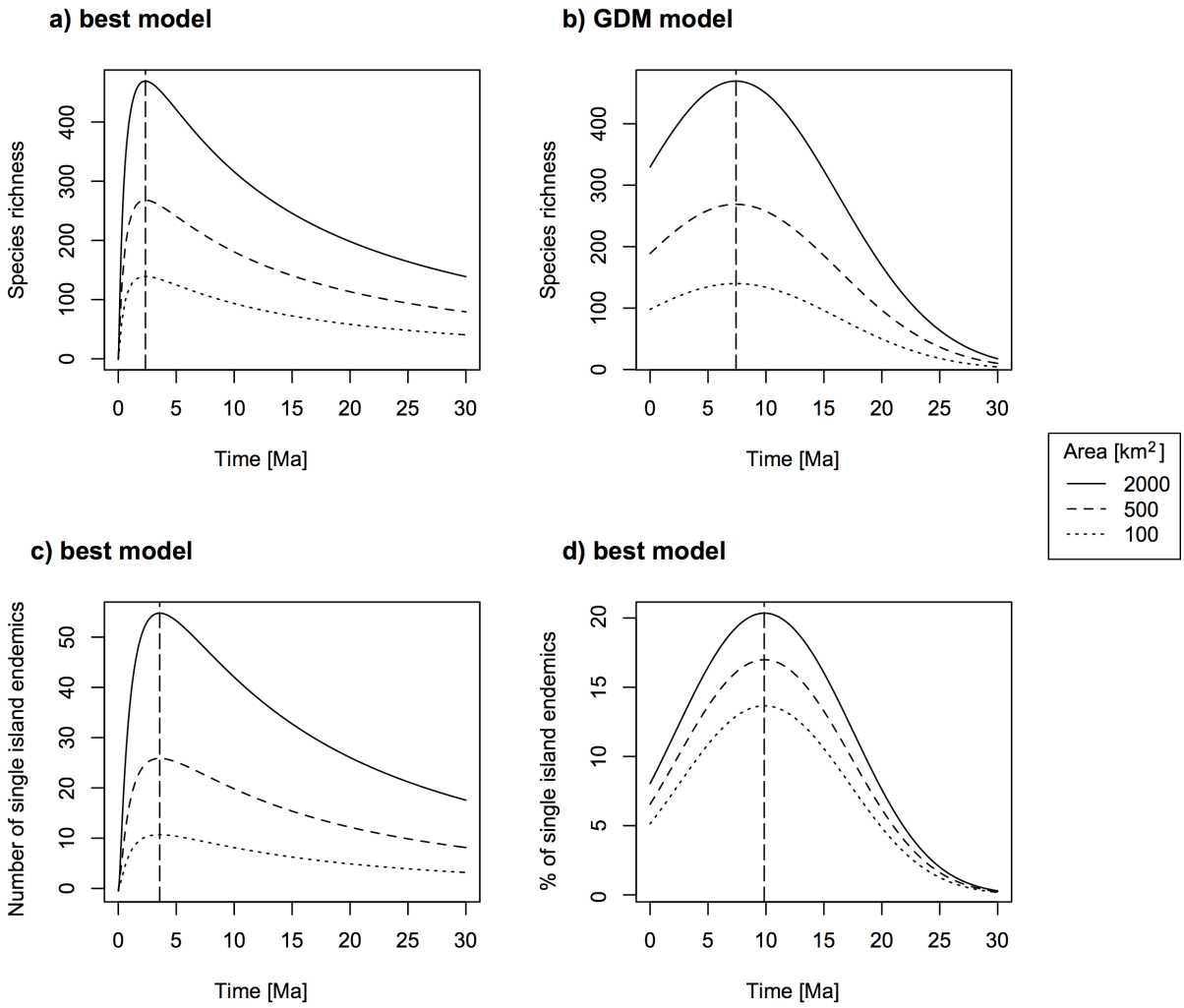

Figure 1: The relation of four diversity related indices with area and time (representing the development phase of a volcanic island). The percentage of SIEs (representing diversification) peaks slightly later than SIE and Di and more than 2.5 million years later than the overall species richness. Predictions were derived from the fixed effects of the mixed effect models of all archipelagos (n = 5, see Table S1) and organism groups (n = 7, see Table S1).

The central idea of the GDM is that volcanic islands exhibit at a certain point in time a given "carrying capacity". Limited resource availability is expected to be valid not only for populations but also for species diversity. This, in turn affects fundamental biogeographical processes such as immigration, extinction and speciation (Whittaker et al. 2007, 2008, 2010).

In the GDM, "carrying capacity" is characterized by area and island elevation (Kalmar and Currie 2006, Whittaker et al. 2007) and additionally by “topographic complexity” (Whittaker et al. 2008). An effect of area is directly included in the ATT^2 model. Our results indicate that it is more important for richness (number of species and SIE) than for diversification (pSIE and DI). Indeed, a direct effect of area on diversification has recently been suggested (Kisel and Barraclough 2010).
"Carrying capacity" is postulated to follow a hump-shaped trajectory during an island’s ontogeny. In the mathematical expression (equation 2) "carrying capacity" is thus represented by time. However, time is not only related to the development of "carrying capacity". Time also needs to pass for processes such as colonisation or speciation to cause a diversity pattern that we can measure and interpret today (e.g. species accumulation, time for speciation see Stephens and Wiens 2003). The fact that species formation via speciation is slower than species accumulation via colonisation is reflected by all indices based on endemic species peaking later than total species richness. This process of species accumulation with time needs to be differentiated from the representation of time for "carrying capacity" associated to the ontogeny of volcanic islands.
The general predictions of the GDM have been confirmed for various taxa (Bunnefeld and Phillimore 2012, Cameron et al. 2013). However, spore-producing plants, which exhibit high dispersal ability, do not show the suggested pattern (Patiño et al. 2013). None of these studies identified the original analyses by Whittaker et al. (2008) to be biased by a misleading significance test. And none of these studied investigated patterns of pSIE. This is likely due to the difficulties involved in the use of percentage values. The percentage of endemic species has a large advantage against overall richness and the number of endemic species. Overall richness has been shown to be highly susceptible to effects of area while the number of endemic species is directly correlated to species richness if one assumes an equal diversification rate per species. The percentage of endemic species is independent from an area-richness relationship. A significant relation between area and pSIE can thus be directly associated to a change in diversification rate (per species) with area. If extinction rate is constant, pSIE is proposed to be a direct measurement of speciation rate per species and time (Emerson and Kolm 2005; Steinbauer et al. 2012, 2013).

Steps ahead

Hypotheses of the GDM are linked to “carrying capacity”. Topographic complexity is taken as a proxy of this resource driven potential (Whittaker et al. 2008). The advantage of this concept in comparison to a process-based model like the one proposed by MacArthur and Wilson (1967) still needs to be proven. In fact, a hump shaped diversity / time relationship does not prove the causal role of a defined “carrying capacity” per time step. MacArthur and Wilson (1967) already discussed the possibility of an upper limit for species richness in the context of “saturation”. They highlighted the importance to build a model where this effect is included in the interaction between immigration and extinction based on the example of Hawaii. On Hawaii (as on all other oceanic islands) colonisation rate was greatly increased after human (especially European) arrival. Non-native species have further increased the overall number of species (MacArthur and Wilson 1967 p.176) therefore questioning the whole concept of “carrying capacity” on these islands.
Alternatively to the GDM, the hump-shape of species richness detected by Whittaker et al. (2007, 2008) could also be associated to a change in the rate of colonisation, extinction or speciation with island topographic complexity, island elevation or environmental diversity. For example, it is very likely that the extinction rate greatly increases after an island has passed the point of maximum topographic complexity (Figure 2). Therefore, relating the change of island characteristics directly to the processes of colonisation, extinction and speciation and not to a concept of “carrying capacity” enables the development of more specific hypotheses.

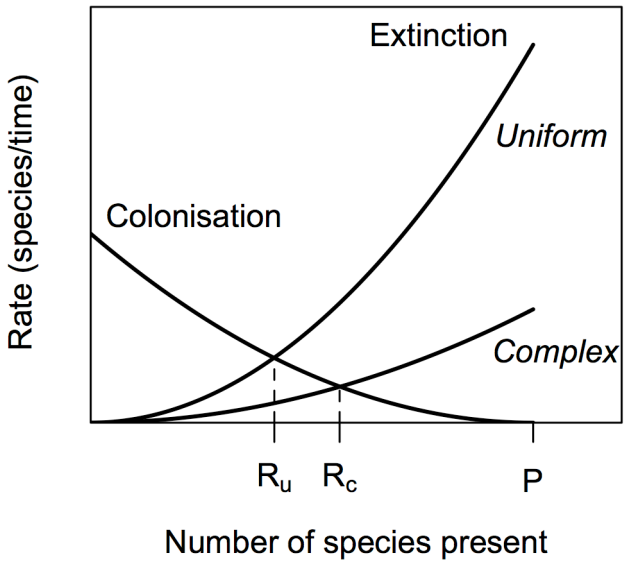

Figure 2: Extinction rate is likely to increase with a decline in topographic complexity. Even if equilibrium conditions are never met due to constant environmental changes, this would be reflected in a decline in species diversity on old oceanic islands. R_U and R_C are theoretical equilibrium conditions in species richness for the island under less and more complex environmental conditions, respectively. After a change in environmental characteristics, the new equilibrium point can be interpreted as an attractor. With time passing, species turnover via immigration and extinction will shift overall species richness towards this value. P denotes a theoretical available regional species pool.

References

Anderson, C.L., Channing, A. & Zamuner, A.B. (2009) Life, death and fossilization on Gran Canaria – implications for Macaronesian biogeography and molecular dating. Journal of Biogeography, 36, 2189-2201.

Bates, D., Maechler, M. & Bolker, B. (2011) lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-40

Brown, J.H. & Lomolino, M.V. (2000) Concluding remarks: historical perspective and the future of island biogeography theory. Global Ecology and Biogeography, 9, 87-92.

Bunnefeld, N. & Phillimore, A.B. (2012) Island, archipelago and taxon effects: mixed models as a means of dealing with the imperfect design of nature's experiments. Ecography, 35, 15-22

Cameron, R.A.D., Triantis, K.A., Parent, C.E., Guilhaumon, F., Alonso, M.R., Ibáñez, M., de Frias Martins, A.M., Ladle, R.J. & Whittaker, R.J. (2013) Snails on oceanic islands: testing the general dynamic model of oceanic island biogeography using linear mixed effect models. Journal of Biogeography, 40, 117-130.

Emerson, B.C. & Kolm, N. (2005) Species diversity can drive speciation. Nature, 434, 1015-1017.

Fattorini, S. (2009) On the general dynamic model of oceanic island biogeography. Journal of Biogeography, 36, 1100-1110.

Fernández-Palacios, J.M., de Nascimento, L., Otto, R., Delgado, J.D., García-del-Rey, E., Arévalo, J.R. & Whittaker, R.J. (2011) A reconstruction of Palaeo-Macaronesia, with particular reference to the long-term biogeography of the Atlantic island laurel forests. Journal of Biogeography, 38, 226–246.

Heaney, L.R. (2000) Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography. Global Ecology and Biogeography, 9, 59–74.

Heaney, L.R. (2007) Is a new paradigm emerging for oceanic island biogeography? Journal of Biogeography, 34, 753–757.

Hortal, J. (2012) Escaping the trap of low sample size in island biogeography. Frontiers of Biogeography, 3.4, 127-129.

Kalmar, A. & Currie, D.J. (2006) A global model of island biogeography. Global Ecology and Biogeography, 15, 72-81.

Kisel, Y. & Barraclough, T.G. (2010) Speciation has a spatial scale that depends on levels of gene flow. The American Naturalist, 175, 316–334.

Lomolino, M.V. (2000) A call for a new paradigm of island biogeography. Global Ecology and Biogeography, 9, 1–6.

MacArthur, R.H. & Wilson, E.O. (1963) An equilibrium theory of insular zoogeography. Evolution 17, 373-387.

MacArthur, R.H. & Wilson, E.O. (1967) The Theory of Island Biogeography. – Princeton University Press, Princeton, NJ.

Millar, R.B., Anderson, M.J. & Tolimieri, N. (2011) Much ado about nothings: using zero similarity points in distance-decay curves. Ecology, 92, 1717-1722.

Patiño, J., Guilhaumon, F., Whittaker, R.J., Triantis, K.A., Gradstein, S.R., Hedenäs, L., González-Mancebo, J.M. & Vanderpoorten, A. (2013) Accounting for data heterogeneity in patterns of biodiversity: an application of linear mixed effect models to the oceanic island biogeography of spore-producing plants. Ecography, in press, doi: 10.1111/j.1600-0587.2012.00020.x

R Development Core Team (2011) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Simberloff, D. (1980) A succession of paradigms in ecology: Essentialism to materialism and probabilism. Synthese, 43, 3-39.

Stahel, W.A. (2002) Statistische Datenanalyse. Eine Einführung für Naturwissenschaftler. 4. Aufl. Vieweg Verlag, Braunschweig/Wiesbaden.

Steinbauer, M.J., Otto, R., Naranjo-Cigala, A., Beierkuhnlein, C. & Fernández-Palacios J.M. (2012) Increase of island endemism with altitude – speciation processes on oceanic islands. Ecography, 35, 23-32.

Steinbauer, M.J., Irl, S. & Beierkuhnlein, C. (2013) Elevation-driven ecological isolation promotes diversification on Mediterranean islands. Acta Oecologica, 47, 52-56.

Stephens, P.R. & Wiens, J.J. (2003) Explaining species richness from continents to communities: the time-for-speciation effect in emydid turtles. The American Naturalist, 161, 112-128.

Triantis, K.A., Borges, P.A.V., Hortal, J. & Whittaker, R.J. (2011) The Macaronesian province: patterns of species richness and endemism of arthropods. Terrestrial arthropods of Macaronesia – Biodiversity, ecology and evolution (ed. by A.R.M. Serrano, P.A.V. Borges, M. Boieiro and P. Oromí), pp. 49–71. Sociedade Portuguesa de Entomologia, Lisbon.

Whittaker, R.J. (2000) Scale, succession and complexity in island biogeography: are we asking the right questions? Global Ecology and Biogeography, 9, 75–85.

Whittaker, R.J., Ladle, R.J., Araújo, M.B., Fernández-Palacios, J.M., Delgado, J.D. & Arevalo, J.R. (2007) The island immaturity - speciation pulse model of island evolution: an alternative to the "diversity begets diversity" model. Ecography, 30, 321–327.

Whittaker, R.J., Triantis, K.A. & Ladle, R.J. (2008) A general dynamic theory of oceanic island biogeography. Journal of Biogeography, 35, 977–994.

Whittaker, R.J., Triantis, K.A. & Ladle, R.J. (2010) A general dynamic theory of oceanic island biogeography: extending the MacArthur-Wilson theory to accommodate the rise and fall of volcanic islands. The Theory of Island Biogeography Revisited (ed. by J.B. Losos and R.E. Ricklefs), pp. 88-115. Princeton University Press, Princeton.

Appendix S1:

Table S1: Adjusted R^2 values and significance (*** for p<0.001; ** for p<0. 01; * for p<0.05.) of the alternative linear regression models. ∩ and ∪ indicate whether the quadratic term in the model formula is significant and negative (indicating "hump shape") or positive (indicating u shape), respectively.

			SR (Species richness of native species)						nSIE (Number of single-island endemics)					
	Island group	Taxon	logATT^2	logAEE^2	LogA	A	LogT	T+T^2	logATT^2	logAEE^2	LogA	A	LogT	T+T^2
a)									b)					
	Canary	arthropods	0.90* ∩	ns	ns	ns	ns	ns	0.85* ∩	ns	ns	ns	ns	ns
	Canary	plants	**0.83*** ∩	ns	ns	ns	ns	ns	**0.84*** ∩	ns	ns	ns	ns	ns
	Canary	snails	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
	Hawaii	arthropods	0.67*	0.61*	**0.71****	ns	0.44*	ns	0.61*	ns	**0.63****	ns	0.35*	ns
	Hawaii	coleoptera	0.64*	0.58*	**0.66****	ns	0.37*	ns	**0.66***	0.56*	0.65**	ns	0.33*	ns
	Hawaii	plants	0.91***	**0.94***** ∩	ns	ns	0.53*	0.61*	**0.75**** ∩	ns	0.42*	ns	ns	ns
	Hawaii	snail	ns	ns	**0.57****	ns	ns	ns	ns	ns	**0.39***	ns	ns	ns
	Galapagos	insects	0.71** ∩	0.60*	0.61**	0.29*	ns	ns	0.49*	ns	0.41*	ns	ns	ns
	Galapagos	insects (so)	**0.64****	0.58*	0.57**	ns	ns	ns	ns	ns	ns	ns	ns	ns
	Galapagos	beetles	**0.74**** ∩	0.60*	0.62***	0.33	ns	ns	0.62**	0.53*	0.57**	0.41*	ns	ns
	Galapagos	plants	**0.79*****	0.73**	0.72***	0.44**	ns	ns	**0.65****	0.58*	0.42**	ns	ns	ns
	Marquesas	plants	**0.90*****	0.88** ∩	0.78***	0.57**	ns	ns	ns	ns	0.49*	0.77***	ns	ns
	Azores	arthropods	**0.79***	0.73*	0.71**	0.74**	ns	ns	ns	ns	0.51*	**0.67****	ns	ns
	Azores	snails	**0.92****	ns	ns	ns	ns	ns	**0.93*****	ns	ns	ns	0.50*	0.91***
			pSIE (Proportion of SIE)						DI (Diversification index)					
	Island group	Taxon	logATT^2	logAEE^2	LogA	A	LogT	T+T^2	logATT^2	logAEE^2	LogA	A	LogT	T+T^2
c)									d)					
	Canary	arthropods	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
	Canary	plants	**0.81*** ∩	ns	ns	ns	ns	ns	**0.94**** ∩	ns	ns	ns	ns	ns
	Canary	snails	ns	ns	ns	ns	ns	0.80* ∩	0.83* ∩	ns	ns	ns	ns	0.80* ∩
	Hawaii	arthropods	**0.71***	0.57*	0.43*	ns	0.43*	0.56*	**0.85****	0.85**	0.83***	ns	0.55**	0.56*
	Hawaii	coleoptera	**0.80****	ns	ns	ns	0.37*	0.79**	**0.90*****	0.82**	0.82***	ns	0.63**	0.65*
	Hawaii	plants	**0.61*** ∩	ns	0.33*	ns	ns	ns	**0.69***	ns	0.60**	ns	ns	ns
	Hawaii	snail	0.64*	**0.92***** ∩	0.65**	ns	0.32*	ns	ns	0.74*	0.53*	ns	ns	ns
	Galapagos	insects	ns	ns	0.34*	ns	ns	ns	**ns**	ns	ns	ns	ns	ns
	Galapagos	insects (so)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	na
	Galapagos	beetles	0.57*	0.49*	0.41*	ns	ns	ns	ns	0.44*	0.39*	ns	ns	ns
	Galapagos	plants	**0.56***	0.51*	0.29*	ns	ns	ns	**0.71****	0.52*	0.38*	ns	0.26*	ns
	Marquesas	plants	ns	ns	0.49*	0.66**	ns	ns	0.77**	**0.82**∩**	0.66**	0.40*	ns	ns
	Azores	arthropods	ns	ns	ns	ns	ns	ns	**0.80*** ∪	ns	0.57*	ns	ns	ns
	Azores	snails	**0.89****	ns	ns	ns	0.53*	0.86**	ns	ns	ns	ns	0.42*	**0.59***

6. Manuscript 5 - Elevation-driven ecological isolation promotes diversification on Mediterranean islands

Acta Oecologica 47 (2013) DOI: 10.1016/j.actao.2012.11.004

Manuel J. Steinbauer[1,2*], Severin D. H. Irl[1,2], Carl Beierkuhnlein[1]

[1] *Department of Biogeography, University of Bayreuth, D-95447 Bayreuth, Germany*
[2] *Department of Disturbance Ecology, University of Bayreuth, D-95447 Bayreuth, Germany*

** Corresponding author: Phone: +49-921-552211, Fax: +49-921-552315*
E-mail address: manuel.steinbauer@uni-bayreuth.de
Postal address: Manuel Steinbauer, Department of Biogeography, University of Bayreuth, Universitätsstraße 30, 95447 Bayreuth

Abstract
The percentage of single island neo-endemic species (an indicator for evolutionary diversification) was found to be independent of geographic distance to the continent in the case of the Aegean archipelago. It was concluded that speciation is independent of geographic isolation, while evolutionary processes are rather enhanced by *habitat heterogeneity*. An island's maximum elevation was used as an indicator for *habitat heterogeneity*. In contrast, we argue that *habitat heterogeneity (= habitat diversity, i.e. the richness in different habitats*) may be positively related to biotic richness, but a positive effect on speciation is yet to be proven. For any other type of heterogeneity, we propose a precise terminology, especially when assessing its effect on speciation processes.
Alternatively, we propose that *elevation-driven ecological isolation* causes the pattern of endemic species on high-elevation islands. Environmental filtering along an elevational gradient differentiates ecosystems, leading to an increase of isolation with elevation. The reason is that comparable ecosystems are much farther apart than is the case for lowland ecosystems. In addition, ecosystems on neighboring islands or on the continent that may be source regions for colonizing species are small in area in high elevations in comparison with low elevation ecosystems. Consequently, an increased speciation rate resulting in a larger percentage of single island endemic species can be expected for higher elevations on islands and high mountains. Support for this *elevation-driven ecological isolation hypothesis* comes from other islands in the Mediterranean region (e.g. Crete and Corsica), where an increase of the percentage of endemic species with elevation has been observed. Thus, the assessment of (genetic-) isolation should incorporate the distance to similar habitats instead of simple land-to-land connections.

Keywords: island biogeography, Crete, environmental filter, speciation, single island endemic species, neo-endemic, habitat heterogeneity, habitat diversity

Abbreviations: pSIE = percentage of single island endemics

1. Increasing isolation and speciation with elevation

Recently, it was claimed that speciation on continental islands is not directly driven by isolation because no relationship between geographical distance to the mainland and the percentage of neo-endemic species was found (Kallimanis et al., 2011). Instead, it was proposed that *habitat heterogeneity* expressed by an island's maximum elevation drives speciation. A positive effect of *habitat heterogeneity* on speciation has been assumed by several studies (Halas et al., 2005; Stuessy et al., 2006). However, we alternatively suggest that elevation controls speciation rather via the effect of *elevation-driven ecological isolation* (sensu Steinbauer et al., 2012a).

Genetic isolation, as especially provided by islands, is reported to support speciation processes (Heaney, 2000). The degree of genetic isolation is, above all, affected by the number of individuals or propagules that are exchanged among populations. Isolation, however, varies between ecosystems depending on the location on the island (Steinbauer et al., 2012a). The geographical distance between landmasses, as applied by Kallimanis et al. (2011), is only reasonable for coastal habitats. Especially high-elevation ecosystems (e.g. Mount Psiloritis [2456 m a.s.l.] on Crete or Monte Cinto [2706 m a.s.l.] on Corsica both reaching far into the alpine zone) differ considerably in their environmental setting from the low-elevation regions on the neighboring continent. Here, the distance to comparable continental ecosystems is a better indicator for the degree of isolation (Steinbauer et al., 2012a). This distance increases with elevation, as comparable mainland ecosystems are likely to be located distant from the coast (Fig. 1). In addition, not only focal island ecosystems but also the related continental ecosystems tend to become smaller in area with elevation. A smaller source region is likewise linked to a decline in the number of arriving colonists (i.e. propagule pressure) (MacArthur and Wilson, 1967), leading to an additional increase of isolation - and thus speciation processes - with elevation on islands. This hypothesis of an *elevation-driven ecological isolation* (sensu Steinbauer et al., 2012a) results in an increase of the percentage of single island endemic species (pSIE) with elevation. pSIE is used as an indicator for diversification processes (Emerson and Kolm, 2005) and its increase with elevation was recently proven for oceanic islands (Steinbauer et al., 2012a).

2. The situation on Crete and other continental islands

While oceanic islands generally consist of volcanic bedrock, continental islands may have a more diverse geological history. They often integrate bedrock from the continental plate that is less susceptible to erosion than bedrock of volcanic origin. Continental islands are often geologically older than oceanic ones.

Elevation-specific datasets for islands in general and for continental islands (i.e. true geographical islands surrounded by water but geologically part of the continental plate) in particular are rare. For continental islands the postulated *elevation-driven ecological isolation* hypothesis can be assessed using data for Crete, the highest of the 19 Aegean Islands that actually contain single island endemic species. Kazakis et al. (2007) highlight the richness in endemic species in higher elevations of Crete. They further report that the percentage of Balkan taxa shows an increase with elevation on Crete, while the proportion of Euro-Mediterranean species tends to decrease. Spiders inhabiting high-elevation ecosystems on Crete are mainly reported to be either palearctic or endemic species, while low elevation spiders tend to be xerophilous and are adapted to high temperatures and aridity (Chatzaki et al., 2005). Trigas et al. (2011) identified an increase of pSIE, for vascular plants with elevation, exceeding 40% in the summit region (i.e. ~2400 m a.s.l.).

Comparable conditions are reported from Corsica. Here, the percentage of endemic species reaches up to 50% in the mountainous and alpine vegetation belts but is below 10% in the lowlands (Gamisans, 1991; Thompson, 2005). On Corsica, many mountain species are interpreted to be evolutionary old arctic-alpine species (Contandriopoulous, 1962) with little colonization of newer species (Thompson, 2005). This indicates that high-elevation ecosystems might serve as refugia for old high mountain taxa that were able to withstand climatic fluctuations during the Pleistocene. In general, the ecological isolation of mountain systems does not

only reduce gene flow between habitats, but also prevents the establishment of new (non-native) species (Thompson 2005). This fact supports the remarkable persistence of established species.

On the Mediterranean islands many low-elevation sites were connected during the Pleistocene via land bridges. However, even under continental conditions high-elevation ecosystems remained isolated as distinct ecosystems, even if they were larger in size due to the downward shift during a colder climate. In consequence, we can expect that the populations of Mediterranean high-mountain island endemics were substantially larger during the glaciation periods than they are today.

The observed increase in the percentage of endemic species with elevation is associated with an overall decrease in species richness of high elevation floras, both on Corsica (Thompson, 2005) and Crete (Greuter, 1972). Their relatively low species richness and the associated unoccupied niches are additional evidence for ecological isolation. Indeed, species diversity of island mountain floras was presumably never as high as that of comparable continental high mountains.

The combination of species-poor ecosystems with "empty niche space" and genetic isolation likely drives increased speciation rates at high elevations on islands. Whittaker and Fernández-Palacios (2007) indicated that ancient continental islands host a higher percentage of endemic species than oceanic islands. Values reaching 40-50% of endemic species in high-elevation ecosystems on Mediterranean islands are comparable to the high-elevation ecosystems of oceanic islands like the Canary Islands (Steinbauer et al., 2012a) or La Réunion (Strasberg et al., 2005).

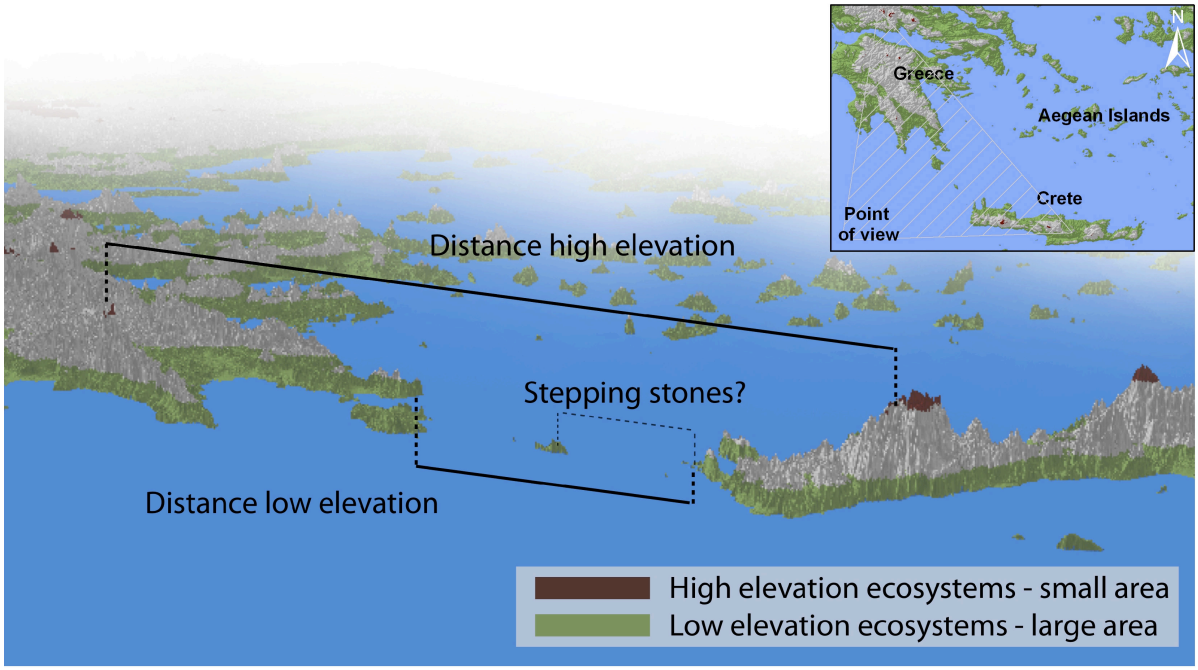

Figure 1. *View of Greece (left, with the Peloponnesus in the background), Crete (right foreground) and the Aegaen Islands (center) from the Southwest (inlay). Green areas display the coastal zone (i.e. 0 -500 m a.s.l.), brown the high-elevation ecosystems (2000 – 2500 m a.s.l.). Obvious is the high isolation of high-elevation ecosystems compared to coastal ones and low-elevation stepping stones. As shown, Crete is the only one of the Aegean Islands actually possessing high-elevation ecosystems. Vertical exaggeration: x 10. (SRTM data provided by NASA; image created in ArcScene 10)*

3. Human influence

An increase of the ratio of endemic species with elevation can be associated with decreasing impact of humans. Endemic species might have gone extinct in low elevations due to the tremendous human pressure on lowland habitats, while endemics could survive in more pristine high-elevation ecosystems (Sarnat and Moreaux, 2010). Losses of endemic species were presumably induced by human overexploitation (Panitsa and Tzanoudakis, 2001). Nevertheless, human influence can hardly explain the increase of pSIE with elevation. The number of endemic species driven to extinction that would be needed in low elevation ecosystems to reach the extraordinary high ratios of high-elevation ecosystems is immense. These hypothetically missing species would need to be new (now unknown) species as community composition differs considerably along elevation due to very strong ecological filters. In fact, the endemic plant species of Greece show narrow geographical and altitudinal distribution ranges (Georghiou and Delipetrou, 2010). Recent studies have emphasized the general tendency to overestimate the magnitude of anthropogenic influence on vegetation composition in the Mediterranean (Collons et al., 2012). Nonetheless, the reported increase of Balkan floral elements on Crete in congruence with a decline in Euro-Mediterranean species along the elevational gradient (Kazakis et al., 2007) can be interpreted in favor for both hypotheses: *human influence* or *elevation-driven ecological isolation*. The higher ratio of Mediterranean species in low elevations on Crete may result from an above-average rate of introduction of Euro-Mediterranean species to low-elevation ecosystems, or from environmental filtering along the elevational gradient favoring mountain species in higher elevations.

4. Isolation via environmental filtering along elevational gradients

Evidence suggests that isolation of continental islands (i.e. located on the shelf close to the continent and consisting of continental parent material) is less effective for inducing speciation than is the case for oceanic islands (volcanic islands on the oceanic crust) (Cody, 2006). This seems to be especially true for the Aegean Islands (Parmakelis et al., 2006; Poulakakis et al., 2008). Yet islands that are located on the shelf of continents are often older than oceanic islands. In addition, the probability for an island to be part of a dense agglomeration of neighboring islands of comparable age is rather high on the shelf. Furthermore, Kallimanis et al. (2011) propose that speciation processes on the Aegean Islands are rather associated to random than to adaptive differentiation (Bittkau and Comes, 2005; Edh et al., 2007; Georghiou and Delipetrou, 2010). Random differentiation is usually induced by very efficient genetic isolation. The distances between coastlines alone can hardly be related to isolation of high-mountain habitats and populations (Fig. 1), owing to the fact that it was likely to be much lower during times of reduced sea level. The strong correlation between maximum island elevation and pSIE on the Aegean Islands identified for neo-endemic species (i.e. in-situ evolution) by Kallimanis et al. (2011) can therefore also hint at *elevation-driven ecological isolation* (senu Steinbauer et al. 2012a) on the archipelago.

However, the phenomenon of elevation-driven isolation is not restricted to island systems. The increase of pSIE with elevation is also reported for continental mountain systems (Kessler et al., 2002; Mallet-Rodrigues et al., 2010) that exhibit strong spatial isolation and genetic distinctness of biota (Mota et al., 2002). Overall, the highest proportions of endemism in the whole Mediterranean region can be found in high mountains (Médail and Quézel, 1997; Verlaque et al., 1997).

5. The role of heterogeneity for speciation

The understanding and definition of the term *habitat* differs among researchers. Partly it is given a species-specific meaning indicating the living conditions of a species' population (e.g. Tscharntke et al. 2012). However, it is also common to apply habitat in a comprehensive way at the community scale. Then, *habitat diversity* is used synonymously to *habitat heterogeneity* and often quantifies the number of vegetation units (see e.g. Tews et al., 2004; Stuessy et al.,

2006; Kallimanis et al., 2011; Triantis et al., 2012) or as the sum of land cover classes (Kisel et al. 2011), which are often correlates of the elevational range. In this case, there is strong evidence that on islands *habitat diversity* (i.e. sum of vegetation units) contributes to both species richness and endemic richness (e.g. Hortal et al., 2009; Kallimanis et al., 2010; Panitsa et al., 2010; Steinbauer and Beierkuhnlein, 2010). Via direct relation high numbers of species are expected to result in a large number of endemic species, if assuming an equal speciation rate for all species.

Here, however, we are interested in how different environmental variables contribute to an increase in speciation rate *per species*, which would be reflected in an increase in the percentage of endemic species per given area. Stuessy et al. (2006) found the proportion of species evolved through adaptive radiation to be positively related to *habitat diversity* (i.e. sum of vegetation units) on islands. Assuming that speciation through adaptive radiation is much faster than random drift, this can be interpreted as an increase of speciation rate *per species* with increasing *habitat diversity*. In consequence there is some evidence that island elevation as a proxy for *habitat diversity* supports diversification processes within islands (Stuessy et al., 2006). Stuessy et al. (2006) identified a strong collinearity between *habitat diversity* and elevation with the latter being the better predictor for the percentage of species evolved through adaptive radiation. Thus we argue that other processes such as the *elevation-driven ecological isolation* are driving adaptive radiation on islands rather then *habitat diversity* per se.

However, the heterogeneity of habitats reflected by differences of environmental properties between and within habitat types may also enhance speciation (Svenning, 2001; Halas et al., 2005). This fact is not covered by the common understanding of *habitat diversity* (i.e. the mere number of habitat types). Environmental micro-heterogeneity may result in genetic differentiation in plants even in very small scales (in some cases even on scales smaller than 1m; Linhart and Grant, 1996; Leimu and Fischer, 2008). The edaphic heterogeneity found within temperate meadows is for instance reported to stimulate within-species differentiation of herbs (Silvertown et al., 1999). Resulting small-scale genetic differentiation facilitates local adaptation by natural selection (Eguiarte et al., 1992). Accordingly, *in situ* speciation should be promoted in "environmentally diverse localities" (Panitsa et al., 2010). Thus we claim that the heterogeneity of the environment is likely to support speciation processes even on very small scales. Approaches towards the quantification of ecological heterogeneity and complexity could address, beside others, microclimatic settings (e.g. Scherrer and Körner, 2011), surface roughness (e.g. Leutner et al., 2012; Steinbauer et al., 2012b), soil types and disturbance regimes (e.g. Buhk et al., 2007). However, detailed investigations and especially a coherent concept and terminology are still missing (see Palmer 1994). While "heterogeneity" as a vague term is already included in ecological theory (Whittaker et al. 2008) it is neither precisely defined nor measured in standardized ways. In fact it is likely that pronounced scale effects (grain and extent; in case of topography in three dimensions), methodological problems and a missing general concept have hindered a profound examination of heterogeneity effects.

6. Conclusion

Assessing the role of isolation for speciation is not trivial and should at least focus on the distance to environmentally similar habitats rather than to terrestrial surfaces or land-to-land connections. In addition, large islands between the focal one and the coast ecosystems might act as both source systems (Fernández-Palacios et al., 2011) and stepping stones. Climatic fluctuations and the associated elevational shift of vegetation will additionally affect the occurrence of endemic species on islands. Climatic changes are also connected to temporal trends in propagule pressure from the continent. In the past, the probabilities of dispersal and gene flow in the Mediterranean have been substantially different from the present (Thompson, 2005). Thus, distance and/or connectivity to refugia, where species could survive long-term climatic fluctuations, can be another good indication for isolation depending on the timeframe associated with the process under focus (Medail and Diadema, 2009).

While *habitat diversity* is directly linked to the size of regional species pools, local environmental heterogeneity is likely to be positively related to speciation processes. However, this assumption is yet to be proven. An appropriate quantification of spatial heterogeneity and of its reflection in ecological complexity is required. Last but not least, a precise wording for spatial and ecological settings is needed in order to identify generality.

Acknowledgements:
We thank Reinhold Stahlmann and Dominik Fischer for their support especially regarding 3D-GIS applications and Kostas Triantis for some critical comments on the manuscript.

References

Bittkau, C., Comes, H.P., 2005. Evolutionary processes in a continental island system: molecular phylogeography of the Aegean Nigella arvensis alliance (Ranunculaceae) inferred from chloroplast DNA. Mol. Ecol. 14, 4065-4083.

Buhk, C., Retzer, V., Beierkuhnlein, C., Jentsch, A., 2007. Predicting plant species richness and vegetation patterns in cultural landscapes using disturbance parameters, Agricult. Ecosys. Environ. 122, 446-452.

Chatzaki, M., Lymberakis, P., Markakis, G., Mylonas, M., 2005. The distribution of ground spiders (Araneae, Gnaphosidae) along the altitudinal gradient of Crete, Greece: species richness, activity and altitudinal range. J. Biogeogr. 32, 813–831.

Cody, M.L., 2006. Plants on Islands: Diversity and Dynamics on a Continental Archipelago. University of California Press.

Collins, P.M., Davis, B.A.S., Kaplan, J.O., 2012. The mid-Holocene vegetation of the Mediterranean region and southern Europe, and comparison with the present day. J. Biogeogr. doi:10.1111/j.1365-2699.2012.02738.x

Contandriopoulous, J., 1962. Recherches sur la flore endémique de la Corse et sur ses origines, Faculté des Sciences de Montpellier.

Edh, K.A., Widén, B., Ceplitis, A., 2007. Nuclear and chloroplast microsatellites reveal extreme population differentiation and limited gene flow in the Aegean endemic Brassica cretica (Brassicaceae). Mol. Ecol. 16, 4972-4983.

Eguiarte, L.E., Perez-Nasser, N., Piilero, D., 1992. Genetic structure, outcrossing rate and heterosis in Astrocaryum mexicanum (tropical palm): Implications for evolution and conservation. Heredity 69, 217-228.

Emerson, B.C., Kolm, N., 2005. Species diversity can drive speciation. Nature 434, 1015–1017.

Fernández-Palacios, J. M., de Nascimento, L., Otto, R., Delgado J.D., García-del-Rey, E., Arévalo, J.R., Whittaker, R.J., 2011. A reconstruction of Palaeo-Macaronesia, with particular reference to the long-term biogeography of the Atlantic island laurel forests. J. Biogeogr. 38, 226–246.

Gamisans, J., 1991. La vegetation de la Corse. Aix-en-Provence. Edisuid.

Georghiou, K., Delipetrou, P., 2010. Patterns and traits of the endemic plants of Greece. Bot. J. Linn. Soc. 162, 130-422.

Greuter, W., 1972. The relict element of the flora of Crete and its evolutionary significance, in: Valentine, D.H., Taxonomy, phytogeography and evolution, London, Academic Press. 161-177.

Halas, D., Zamparo, D., Brooks, D.R., 2005. A historical biogeographical protocol for studying biotic diversification by taxon pulses. J. Biogeogr. 32, 249–260.

Heaney, L.R., 2000. Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography. Global Ecol. Biogeogr. 9, 59–74.

Hortal, J., Triantis, K.A., Meiri, S., Thébault, E., Sfenthourakis, S., 2009. Island Species Richness Increases with Habitat Diversity. Am. Nat. 174, 205–217.

Kallimanis, A.S., Bergmeier, E., Panitsa, M., Georghiou, K., Delipetrou, P., Dimopoulos, P., 2010. Biogeographical determinants for total and endemic species richness in a continental archipelago. Biodivers. Conserv. 19, 1225-1235.

Kallimanis, A.S., Panitsa, M., Bergmeier, E., Dimopoulos, P., 2011. Examining the relationship between total species richness and single island palaeo- and neo-endemics. Acta Oecol 37, 65-70.

Kazakis, G., Ghosn, D., Vogiatzakis, I.N., Papanastasis, V.P., 2007. Vascular plant diversity and climate change in the alpine zone of the Lefka Ori, Crete. Biodivers. Conserv. 16, 1603–1615.

Kessler, M., 2002. The elevational gradient of Andean plant endemism: varying influences of taxon- specific traits and topography at different taxonomic levels. J. Biogeogr. 29, 1159–1165.

Kisel, Y., McInnes, L., . Toomey, N.H., Orme, C.D.L. 2011. How diversification rates and diversity limits combine to create large-scale species –area relationships. Phil. Trans. R. Soc. B. 366, 2514-2525

Leimu, R., Fischer, M., 2008. A meta-analysis of local adaptation in plants. PLoS ONE 3, e4010.

Leutner, B., Steinbauer, M.J., Müller, C.M., Früh, A.J., Irl, S., Jentsch, A., Beierkuhnlein, C., 2012. Mosses Like It Rough - Growth Form Specific Responses of Mosses, Herbaceous and Woody Plants to Micro-Relief Heterogeneity, Diversity, 4, 59-73.

Linhart, Y.B., Grant., M.C., 1996. Evolutionary significance of local genetic differentiation in plants. Ann. Rev. Ecol. Syst. 27, 237-277.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ.

Mallet-Rodrigues, F., Parrini, R., Pimentel, L.M.S., Bessa, R. 2010. Altitudinal distribution of birds in a mountainous region in southeastern Brazil. Zoologica 27, 503–522.

Médail, F., Diadema, K., 2009. Glacial refugia influence plant diversity patterns in the Mediterranean Basin. J. Biogeogr. 36, 1333–1345.

Médail, F., Quézel, P., 1997. Hot-spots analysis for conservation of plant biodiversity in the Mediterranean Basin. Ann. Mo. Bot. Gard. 84, 112-127.

Mota, J.F., Pérez-García, F.J., JiMénez, M.L., Amate, J.J., Penãs, J. 2002. Phytogeographical relationships among high mountain areas in the Baetic Ranges (South Spain). Global Ecol. Biogeogr. 11, 497 – 504.

Palmer, M.W. 1994. Variation in species richness: towards a unification of hypotheses. Folia Geobot. Phytotax. 29, 511-530.

Panitsa, M., Tzanoudakis, D., 2001. A floristic investigation of the islat group Sarki and Lipsi (East Aegean Area, Greece). Folia Geobot. 36, 265-279.

Panitsa, M., Trigas, P., Iatrou, G., Sfenthourakis, S., 2010. Factors affecting plant species richness and endemism on land-bridge islands e an example from the East Aegean archipelago. Acta Oecol. 36, 431-437.

Parmakelis, A., Stathi, I., Chatzaki, M., Simaiakis, S., Spanos, L., Louis, C., Mylonas, M., 2006. Evolution of Mesobuthus gibbosus (Brulle, 1832) in the north-eastern Mediterranean region. Mol. Ecol. 15, 2883-2894.

Poulakakis, N., Pakaki, V., Mylonas, M., Lymberakis, P., 2008. Molecular phylogeny of the Greek legless skink Ophiomorus punctactissimus (Squamata: Scincidae): the impact of the Mid-Aegean trench in its phylogeography. Mol. Phylogenet. Evol. 47, 396-402.

Sarnat, E.M., Moreaux, C.S., 2010. Biogeography and morphological evolution in a Pacific island ant radiation. Mol. Ecol. 20, 114-130.

Scherrer, D., Körner, C., 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. J. Biogeogr. 38, 406-416.

Silvertown, J., Dodd, M.E., Gowing, D.J.G., Mountford, J.O., 1999. Hydrologically defined niches reveal a basis for species richness in plant communities. Nature 400, 61-63.

Steinbauer, M.J., Beierkuhnlein, C., 2010. Characteristic pattern of species diversity on the Canary Islands. Erdkunde 64, 57-71.

Steinbauer, M.J., Otto, R., Naranjo-Cigala, A., Beierkuhnlein, C., Fernández-Palacios, J.M., 2012a. Increase of island endemism with altitude – speciation processes on oceanic islands. Ecography 35, 23-32.

Steinbauer, M.J., Gohlke, A., Mahler, C., Schmiedinger, A., Beierkuhnlein, C., 2012b. Quantification of wall surface heterogeneity and its influence on species diversity at medieval castles - implications for the environmentally friendly preservation of cultural heritage, J. Cult. Herit., accepted - doi:10.1016/j.culher.2012.06.003

Strasberg, D., Rouget, M., Richardson, D.M., Baret, S., Dupont, J., Cowling, R.M., 2005. An assessment of habitat diversity and transformation on La Réunion Island (Mascarene Islands, Indian Ocean) as a basis for identifying broad-scale conservation priorities. Biodivers. Conserv. 14, 3015-3032.

Stuessy, T.F., Jakubowsky, G., Salguerò Gómez, R., Pfosser, M., Schlüter, P.M., Fer, T., Sun, B.Y., Kato, H., 2006. Anagenetic evolution in island plants. J. Biogeogr. 33, 1259–1265.

Svenning, J.C., 2001. On the Role of Microenvironmental Heterogeneity in the Ecology and Diversification of Neotropical Rain-Forest Palms (Arecaceae). The Botanical Review 67, 1-53.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., Jeltsch, F. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J. Biogeogr. 31, 79–92.

Thompson, J.D., 2005. Plant evolution in the Mediterranean, Oxford University Press, New York.

Triantis, K.A., Hortal, J., Amorim, I., Cardoso, P., Santos, A.M.C., Gabriel, R., Borges, P.A.V., 2012. Resolving the Azorean knot: a response to Carine & Schaefer (2010). J. Biogeogr. 39, 1179-1184.

Trigas, P., Panitsa, M., Turland, N., Tsiftsis, S., 2011. Elevational gradient of vascular plant species richness and endemism in Crete. Poster 248 at the Fifth Biennial Conference of the International Biogeography Society, Irakleion, Crete, Greece

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H., Westphal, C., 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biol. Rev. 87, 661–685.

Whittaker, R.J., Fernández-Palacios, J.M., 2007. Island Biogeography: Ecology, Evolution, and Conservation, 2nd eds. Oxford University Press, Oxford.

Whittaker, R.J., Triantis, K.A., Ladle, R.J,. 2008. A general dynamic theory of oceanic island biogeography. J. Biogeogr. 35, 977–994.

Verlaque, R., Aboucaya, A., Cardona, M.A., Contandriopoulos, J., 1997. Quelques exemples de speciation insulaire en Méditerranée occidentale. Botanika Chronika 10, 137-154.

7. Manuscript 6 - Quantification of wall surface heterogeneity and its influence on species diversity at medieval castles – implications for the environmentally friendly preservation of cultural heritage

Journal of Cultural Heritage 14 (2013) DOI: 10.1016/j.culher.2012.06.003

Manuel Jonas Steinbauer[a,b], Andreas Gohlke[a], Christine Mahler[a], Andreas Schmiedinger[a], Carl Beierkuhnlein[a]

[a] Dept. of Biogeography, University of Bayreuth, D-95447 Bayreuth, Germany
Manuel.Steinbauer@uni-bayreuth.de, Andreas.Gohlke@uni-bayreuth.de, c.mahler@gmx.net, agrobiol.schmiedinger@t-online.de, Carl.Beierkuhnlein@uni-bayreuth.de
[b] Corresponding author

Address of correspondence: Manuel Steinbauer, University of Bayreuth, Universitätsstraße 30, 95447 Bayreuth
Phone: +49 921-55-2299; fax: +49 921-55-2315.
E-Mail address: Manuel.Steinbauer@uni-bayreuth.de

Abstract
Historic buildings are important for cultural history and provide a variety of habitats for animals and plants. Especially structural heterogeneity of wall surfaces is percived to support biological diversity. Nevertheless, in traditional approaches goals of biodiversity preservation and monument restoration are perceived to interfere and to be mutually exclusive. As a consequence, priority is often given to constructional restoration accepting the loss of local populations and biodiversity.
At walls of medieval castles, including an experimental restoration project where conventional and less intensive restoration techniques were applied, we relate species composition and richness to wall properties. Especially wall surface structure is quantified using a novel approach. The study focuses on lichens, mosses and vascular plants.
Boosted regression tree analyses and non-metric multidimensional scaling techniques are applied to detect the influence of abiotic site conditions on biodiversity.
We find species richness to be promoted by wall surface heterogeneity. However, species composition is more affected by restoration approaches than species richness. Lichen composition varies considerably while vascular plants and mosses are less affected by wall properties.
We suggest strategies that are combining both societal targets, the preservation of historic monuments and of species diversity. Careful restoration is capable of supporting both, the maintenance of cultural heritage and of rare and unique anthropogenic habitats. Wall surface heterogeneity needs to be witnessed for both aspects as it affects both species composition as well as the effectiveness of cleaning methods.

Keywords: biodegradation, biodeterioration, historic buildings, monuments, nature conservation, wall vegetation

1. Introduction and research aims

The preservation of historic monuments and buildings, which represent a country's cultural heritage, constitutes a high societal priority. Future generations must have the opportunity to witness former social structures, the endeavour, aesthetic sentiments and architectural achievements of their ancestors.

Another societal priority, even affirmed in international contracts, is the concept of maintaining biodiversity. Many rare and protected species are bound to nutrient-poor habitats with specific microclimatic conditions such as rocks. Others depend on low disturbance frequency and long-term stable site conditions. Both preconditions are rarely found in cultural landscapes but given at castles and ruins. In Central Europe, many of such anthropogenic habitats exist since centuries.

Whenever both societal ambitions meet at the same object, like an old castle or city wall, they tend to exclude each other. Frequently, prioritisation leads to withdrawal at the side of nature conservation. It is a widely held but unproven belief that all plants, fungi, lichens or animals are causing damage to historic monuments.

Besides the aesthetic surplus, which old castles or city walls can gain through plant cover [1], old monuments often provide habitats for highly specialised animals and plants [2,3]. An influence of the surface structure of walls on biological diversity is documented [4,5]. However, approaches are rare that quantify the influence of structural properties on biological diversity [but see 6,7]). A sound statistical proof for a linkage between biotic diversity and heterogeneity of wall surfaces is still missing.

Modern building techniques are avoiding open joints and niches that serve for instance as protected hiding places for animals but also as germination site for plants. Specific mural vegetation is hence restricted to old constructions. Despite this, it is surprisingly uncommon to see buildings as valuable habitats for biota that require precaution during restoration processes.

During the course of constructional restoration at (historical) buildings dry masonry walls are often jointed, cracks are filled with grounding mortar and the surfaces are cleaned. In consequence, the characteristic mural vegetation as well as habitats of many insects and animal species (e. g. birds and bats) are lost.

Here, we study four medieval castles according to impacts of different restoration treatments on plant communities in order to evaluate the impacts of restoration techniques. To assess best practice restoration techniques for biological diversity we investigated the influence of wall structures on floristic diversity.

2. Material and Methods

2.1 Study area and castles

The study area (Figure 1) is located in Upper Franconia and is characterised by low mountain ranges. The studied fortress "Festung Rosenberg" and the castles "Giechburg", "Burg Waischenfeld" and "Burg Rabenstein" differ in regard to history, climate and landscape traits. As the monuments were constructed with stones from local parent material, the building material is characteristic for the landscape matrix of the monuments. Table 1 provides an overview on abiotic factors and historic characteristics of the examined castles.

2.2 Vegetation data and sample design

Vegetation and related environmental parameters were sampled on seven walls of the four selected castles (table 1) summarising a variety of different monument restoration treatments (table 2). Of special interest is Festung Rosenberg, where different restoration techniques were applied on three parts of the front wall of "Waffenplatz Philipp" in 2001. Each restoration technique was applied on a 11x4 m² sized part of the wall (Figure 2). During the **environmental sound restoration** only woody plants were removed. All remaining vascular plants, mosses and lichens were left on the stones and within gaps. The humus layer on the wall coping was lifted and refitted after restoration work. Wall surface was only cleaned on those places where

restoration was conducted. Grouting was reduced to a necessary minimum. For the **conventional restoration** all plant cover on the wall and the humus layer on the wall coping was removed. The wall surface and gaps were cleaned entirely with superheat stream. Gaps larger one centimetre were grouted. Surface defects were closed using epoxide resin while imbued and vulnerable areas were closed using common lime-cement mortar. The third application was a **compromise solution** between the two former mentioned methods. While mosses and lichens were left in the gaps, woody plants, herbs and grasses were removed. The humus layer was lifted and refitted after restoration work. Only those places were restoration was conducted were cleaned with superheat stream. Grouting was reduced to a necessary minimum [3]. Impacts on wall flora, feasibility and costs of conservation are depicted.

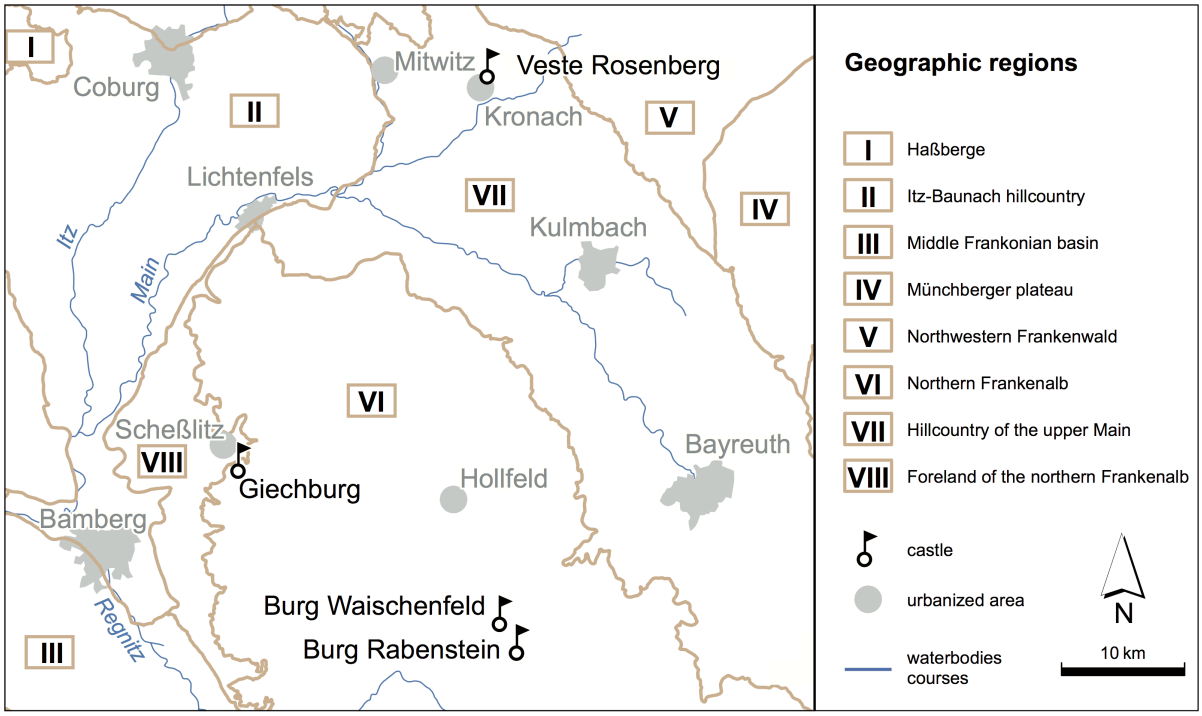

Figure 1: *Study area situated in Upper Frankonia. Reinhold Stahlmann, adapted from [57]*

Temperature and water availability on a wall is closely related to its aspect [8]. Thus, species composition of vascular plants, mosses and lichens often varies strongly between north- and south-facing walls [9,10]. Even if some studies did not find aspect to significantly influence plant cover [11], in our study the examined walls are microclimatically standardized to south and south-west orientation.

The applied plot size of 1 m² is regarded to represent an adequate plot size for wall vegetation (including mosses and lichens) [6]. Via stratified random sampling three plots were placed on the upper and lower parts of each castle wall, respectively. This approach enabled a separate sampling of the upper wall part that is characterised by extreme drought stress, as well as of the lower wall parts with high disturbance intensity and nutrient inputs [2]. Altogether 42 plots were established (6 on each wall) and recorded in 2006 and 2007 (Lichens only 2007, see appendix). Species frequencies were assessed. Each plot was divided in 25 sub plots of 0.04 m^2 size and species presence/absence for vascular plants, mosses and lichens were recorded. Plant records of 2006 and 2007 were summarised taking the mean frequency of a plant species in a specific plot of both years. Nomenclature follows Oberdorfer [12] for vascular plants, Frahm and Frey [13] for mosses and Wirth [14] for lichens.

Table 1: *Abiotic conditions and some history of the examined castles.*

Rabenstein (limestone, 390 m a.s.l., 688 mm annual precipitation, 7.9°C mean temperature). First mentioned AD 1188 was founded by the Edelfreien von Waischenfeld to protect the trading roads coming from the Pegnitz valley in the south [58]. The castle was heavily damaged or destroyed and rebuild several times (Städtekrieg of 1388, Fürstenkrieg 1460-1462, Thirty Years' War 1618–1648) and its holders changed. Since 1976 it is used as a hotel. [59]

Waischenfeld (limestone, 401 m a.s.l., 688 mm annual precipitation, 7.9°C mean temperature) first mentioned AD 1122, belonged to the Edelfreien von Waischenfeld before it changed holders several times. The castle was destroyed in 1430 (Hussite Wars) and plundered in 1553 (Margrave War) but endured the Thirty Years' War undamaged. The wall and a 1754 build palace have been restored while remains of the original palace were removed in 1876. The castle now belongs to the city of Waischenfeld and hosts gastronomy and a museum. [59]

Giechburg (limestone/sandstone, 530 m a.s.l., 701 mm annual precipitation, 7.6°C mean temperature) first mentioned AD 1125 is build on a hill already populated in prehistoric times. The castle was destroyed and rebuild several times (1430 Hussite Wars, 1525 German Peasants' War, 1553 second Margrave War). The current walls and towers date back to fortifications of Fürstbischof Johann Philipp von Gebsattel in 1599-1609. The Giechburgt withstood the Thirty Years war but was nearly destroyed around 1800 by a royal Bavarian inspector who wanted to create a "romantic ruin" by removing the roof. Now, the Giechburg belongs to the county of Bamberg and hosts gastronomy and exhibitions. [59]

Festung Rosenberg (sandstone , 378 m a.s.l., 660 mm annual precipitation, 7.8°C mean temperature) was the northward stronghold of the Bistum Bamberg and protected the strategically important trading routs. First towers were build AD 1128-1130 and later on fortified. The name Rosenberg is first mentioned AD 1249. It became a bishop`s district castle in the 14th century. The second wall was build end of the 15th century. Neither the Hussits, the enemies of the Margrave nor the Swedish forces in the Thirty Years War were able to conquer the stronghold. The pentagon shaped present outer wall was build AD 1656-1700. The fortress was under use by Napoleons armies, Bavarian military, and served in the first world war 1915-1918 as a prison hosting among others Charles de Gaulle. Concrete and steel work was done in parts of the fortress during second world war. Today the Rosenberg hosts a youth hostel, gastronomy and a museum. [60,61]

Table 2: *Size of sampled castle walls and associated restoration techniques. On each wall six plots of 1m² where established.*

Castle	*Restoration type*	*Wall size*	*Abbreviation*
Waischenfeld	conventional restoration 30 - 40 years before sampling	11 x 4 m²	Wfd
Giechburg	conventional restoration	11 x 4 m²	Gbg
Rabenstein	conventional restoration	3 x 2.80 m²	Rsn cr
Rabenstein	no restoration	11 x 3 m²	Rsn nr
Rosenberg	conventional restoration	11 x 4 m²	Rbg cr
Rosenberg	environmental sound restoration	11 x 4 m²	Rbg er
Rosenberg	compromise solution	11 x 4 m²	Rbg cs

2.3 Abiotic variables

While exposition was held constant at all sampling sites, other abiotic influences, namely water availability, the quality of substrate, and surface structure of the wall were analysed in detail.

Quality of building material (stones and mortar) is influencing the vegetation on walls for instance via pH, nitrate- or calcium-availability [9,15]. Therefore substrate samples (ca. 1-2 cm³) were analysed for each plot. the content of sodium, potassium, calcium, magnesium, ammonium as well as fluoride, chloride, nitrate, phosphate and sulphate was measured by ion chromatography.

To estimate the available water electric conductivity was measured four times per plot. In addition, high resolution infrared photos were taken. However, detailed analyses of the resulting estimates of moisture indicated that both methodologies are not providing reliable results and were thus not included in further analyses.

Figure 2: *Testing wall with three different restoration techniques at "Waffenplatz Philipp" on Festung Rosenberg. Photo Alex Ulmer.*

2.4 Wall structure

To quantitatively record the structure of wall surface a grid of profile drawings comparable to elevation profiles in landscapes was found to be most suitable to elaborate metrics that could quantify the structure of the wall. The profiles were gained via a contact based contour measurement sensor (Figure 3a). This approach is not biased by insolation and shadow [16]. For each plot three direction and cross direction profiles of 90 cm length were conducted in a standardised procedure. The profiles were digitalised with a resolution of 1 mm (Figure 3 a, b). Based on these profiles a variety of different parameters that adequately resemble the structural heterogeneity of the wall surface were calculated (Table 3). If not mentioned differently, the mean value of those parameters per plot was taken for further calculations.

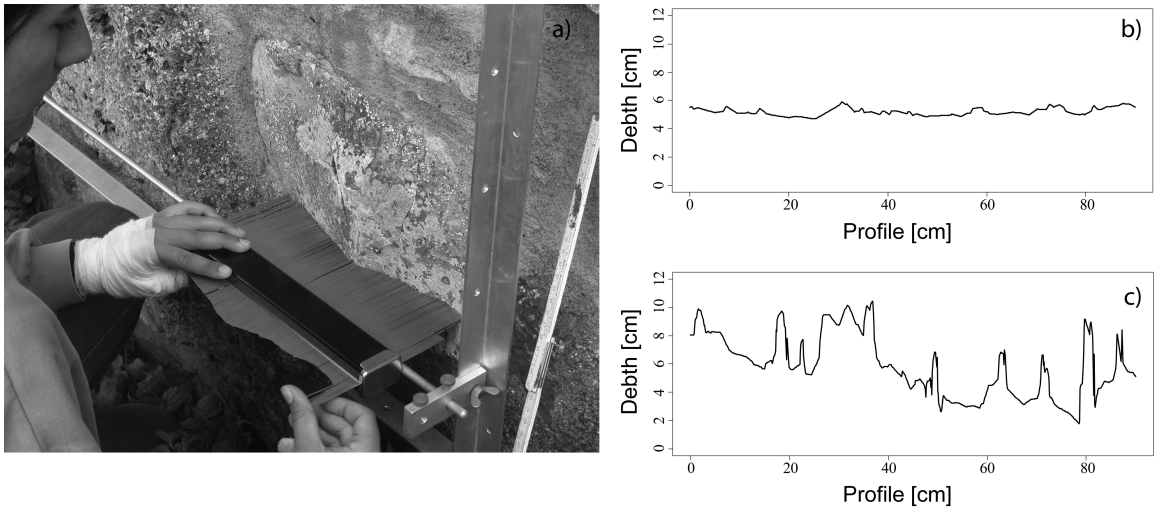

Figure 3: *Surface structure of each plot is gained via three direction and cross direction profiles of 90 cm length. A frame supports standardised measurement (a). Comparison of profiles from a plot (b)at the Festung Rosenberg (compromise solution) and a not renovated plot at Burg Rabenstein (c).*

2.5 Calculations

Environmental variables were standardised (scaled to zero mean and unit variance). All analyses were performed in the statistical program R [17].

Boosted regression trees were used to detect drivers of species richness for all groups (vascular plants + mosses + lichens) jointly as well as separately. All environmental variables were included as predictors. Boosted regression trees were calculated using function gbm.step (gbm 1.6-3) [18]. Model settings as well as summary statistics can be depicted from table 4.

Nonmetric Multi-dimensional Scaling (NMDS) was used to visualise the similarity in species abundance and composition of the plots. The applied Bray-Curtis index is independent from the data distribution and thus ideal for non normal distributed data [19]. By using NMDS the number of dimensions in the ordination space has to be defined a priori. Two dimensions were chosen to facilitate visualisation. Quality of a NMDS can be estimated by the stress value. Low stress values indicate a good fit of the distances between the samples to the dissimilarities of

species assemblages. Stress values below 20 are considered to yield acceptable results [19]. Stress values were 15 for all vegetation, 13 for vascular plants, 12 for bryophytes and 11 for lichens. The applied function metaMDS (vegan 1.17-1) chooses a starting configuration close to a local stress optimum. Iteratively new configurations are calculated and compared to previous results using Procrustes-test to obtain an optimal value [20]. Correlation between measured environmental variables (abiotic and structural) and the first two NMDS axes was assessed with squared correlation coefficient as the goodness of fit statistic. A permutation test with 10,000 iterations was applied to assess significance. Only relevant variables ($p \leq 0.01$) were visualised. To evaluate the contribution of single species groups (vascular plants, bryophytes, lichens) to the overall pattern of combined vegetation, NMDS axes scores of combined and separated analyses were correlated using Pearson correlation.

Table 3: *The below described coefficients were used to measure the structural heterogeneity of the wall surface. For each plot six profiles of 90 cm length were measured (three direction and three cross direction). The mean of the coefficient values of all six profiles were taken as the plot value for calculation. The lengths of the profile line was not suitable for a comparison as many small scale variations in surface structure lead to comparable values as few large scale variations.*

name	description	formula
surface heterogeneity *(variation coefficient)*	The *variation coefficient* indicates variation in depths. It is a normalised measure of dispersion. The larger the value, the more different are the depths values from their mean.	$vc = \frac{\delta}{\bar{x}}$ δ : standard deviation $\bar{x}$: mean value of depths
5 cm surface fluctuation *(DeltaT5)*	*DeltaT5* measures the change in depth per 5 cm: The larger the value, the deeper are the joints, the more heterogenic is the surface.	$DeltaT5 = \frac{\sum_{i/5cm}^{90cm} \lvert x_i - x_{i-5cm} \rvert}{18}$ x_i: value of depths
maximum joint depths	Maximum positive deviance from the mean: the deepest joint or gab in the wall.	$md = \max(x_i - \bar{x})$ x_i: value of depths $\bar{x}$: mean value of depths
Joint frequency *(intersection points)*	The number of *intersection points* with the fictive mean line. A flat wall with few joints will have less intersection points than a rubble masonry.	$ip = \sum_{0}^{N} (x_i - \bar{x}) \cdot (x_{i+1} - \bar{x}) < 0$ x_i: value of depths $\bar{x}$: mean value of depths
surface smoothness *(autocorrelation)*	The *autocorrelation* measures the probability that joints, gabs and other surface irregularities only vary within a certain range. Lag values of 1, 3, 5 and 10 cm (see equation) were applied.	$r = \frac{\sum_{i=1}^{n-\tau} (x_i - \bar{x}) \cdot (x_{i+\tau} - \bar{x})}{\sum_{i=1}^{n} (x_i - \bar{x})^2}$ x_i: value of depths (1mm difference) τ : lag value (here 1, 3, 5 or 10cm) $\bar{x}$: mean value of depths
fine structure *(periodicity)*	Slope of the log transformed periodogram (function in frequency space after Fourier transformation). Measures recurring fine and coarse structures of the wall surface. The larger the value the finer the structures and the less large scale surface fluctuations.	$F(\lambda) = \sum_i x_i \cdot \cos(\pi \cdot \lambda \cdot i) + \sum_i x_i \cdot \sin(\pi \cdot \lambda \cdot i)$ $F(\lambda)$: fourierfunction x_i: value of depths (1mm difference) λ : frequence

Table 4: *Summary statistics of boosted regression tree analysis for species richness. In all model runs bag fraction was set to 0.75 and tree complexity to 5.*

	all vegetation	vascular plants	mosses	lichens
Learning rate	0.0015	0.005	0.0015	0.005
Step size	50	50	50	25
Number of trees	1850	1700	1550	1600
Mean total deviance	8.642	5.812	2.738	1.27
Mean residual deviance	2.232	0.269	1.210	0.165
Estimated CV deviance	5.389	2.761	2.429	1.120
	(se: 1.314)	(se: 0.637)	(se: 0.571)	(se: 0.213)
Training data correlation	0.905	0.980	0.814	0.953
CV correlation	0.670	0.789	0.424	0.420
	(se: 0.096)	(se: 0.064)	(se: 0.168)	(se: 0.171)

3. Results

3.1 Environmental characteristics of wall substrate

Among the interrelations of variables measuring wall chemistry and those measuring wall structure the Pearson product moment correlation of pH with "surface heterogeneity" (r^2=0.54***, negative) as well as "5 cm surface fluctuations" (r^2=0.50***, positive) is of special interest.

The pH values of the stones vary between pH 6.5 and pH 9.6. At the Giechburg and the Burg Waischenfeld values of pH 8 were measured, while the pH value of 8.5 at Burg Rabenstein is slightly higher. The pH value at the castles build from sandstone showed values between pH 6.7 and pH 7.9 (mean value: pH 7.2). The pH of mortar was around pH 8.

The ammonium concentration of construction stones correlates negatively with the pH (r^2=0.17**).

Chloride, sodium and sulphate relate to the corresponding salt ions $NaSO_4$ and NaCl. The corresponding contents in mortar and stones are highly correlated with r^2 up to 0.80. The highest salt contents were found at the Giechburg. The values of the other castles did not differ significantly.

3.2 Species richness and composition

In general the species richness of all vegetation at the investigated walls (figure 4, table 5) is high on surfaces with a high number of joints (BRT results in figure 5, table 4 for summary statistics). However, in contrast to our expectations, larger irregularities are associated with low species numbers. The vascular plants are mainly responsible for this result. "5 cm surface fluctuations" is one of the most important predictors for this group of species. The index "5 cm surface fluctuations" has a negative Pearson's product-moment correlation with "surface heterogeneity" (r^2=0.37***) and a positive correlation with "fine structure" (r^2=0.21**). The negative Pearson's product-moment correlation of "5 cm surface fluctuations" is much stronger with cumulative abundance (r^2=0.24***) than with species richness (r^2=0.06$^{\text{not sig.}}$). Increasing "surface heterogeneity" is followed by an increase in richness of bryophytes while the number of lichens decreases.

Richness of the whole vegetation seems to be independent from pH despite a sudden drop in species numbers between pH 7.5 and 8. The opposite pattern can be identified for calcium and magnesium, where an increase is aligned with more species. Here again bryophytes behave diametrically to lichens with the later increasing in richness with calcium availability while the number of mosses declines. Interestingly an increase in calcium content of the mortar (not shown for lichens) enhances species richness in both groups. Sulphate in building stones is connected with low species diversity.

Table 5: *Occurrence of vascular plants, mosses and lichens on all Walls in 2007.*

Species	Gbg	Wfd	Rsn cr	Rsn nr	Rbg er	Rbg cr	Rbg cs
Vascular plants							
Asplenium ruta muraria	x	x		x	x	x	
Asplenium trichomanes				x			
Brachypodium pinnatum					x	x	x
Calystegia sepium					x		x
Chelidonium majus			x	x			
Cymbalaria muralis			x	x	x	x	x
Epilobium montanum					x	x	x
Festuca ovina agg.					x	x	
Galium album					x		
Geranium robertianum				x		x	
Geum urbanum			x				
Impatiens parviflora				x			x
Lamium maculatum				x			
Poa compressa		x	x		x		x
Poa nemoralis				x	x		x
Rubus fruticosus agg.						x	x
Taxus baccata				x			
Urtica dioica		x	x	x	x	x	x
Verbascum thapsus						x	
Mosses							
Barbula rigidula					x		
Brachythecium rutabulum						x	
Brachythecium velutinum	x				x		
Bryum caespiticium						x	
Bryum capillare			x	x	x	x	x
Grimmia pulvinata		x					
Homalothecium sericeum		x	x	x	x	x	x
Leptobryum pyriforme				x			
Schistidium apocarpum		x					
Tortella tortuosa				x		x	
Tortula muralis	x	x	x	x	x	x	x
Lichens							
Caloplaca cirrochroa			x	x			
Caloplaca citrina	x	x	x	x	x	x	x
Caloplaca decipiens				x			
Caloplaca flavescens		x					
Cladonia pyxidata					x	x	x
Collema crispum			x				
Lecanora dispersa	x	x	x	x		x	x
Lecidella stigmatea		x	x		x	x	x
Lepraria eburnea					x		x
Leproloma vouauxii					x		x
Verrucaria nigrescens			x				

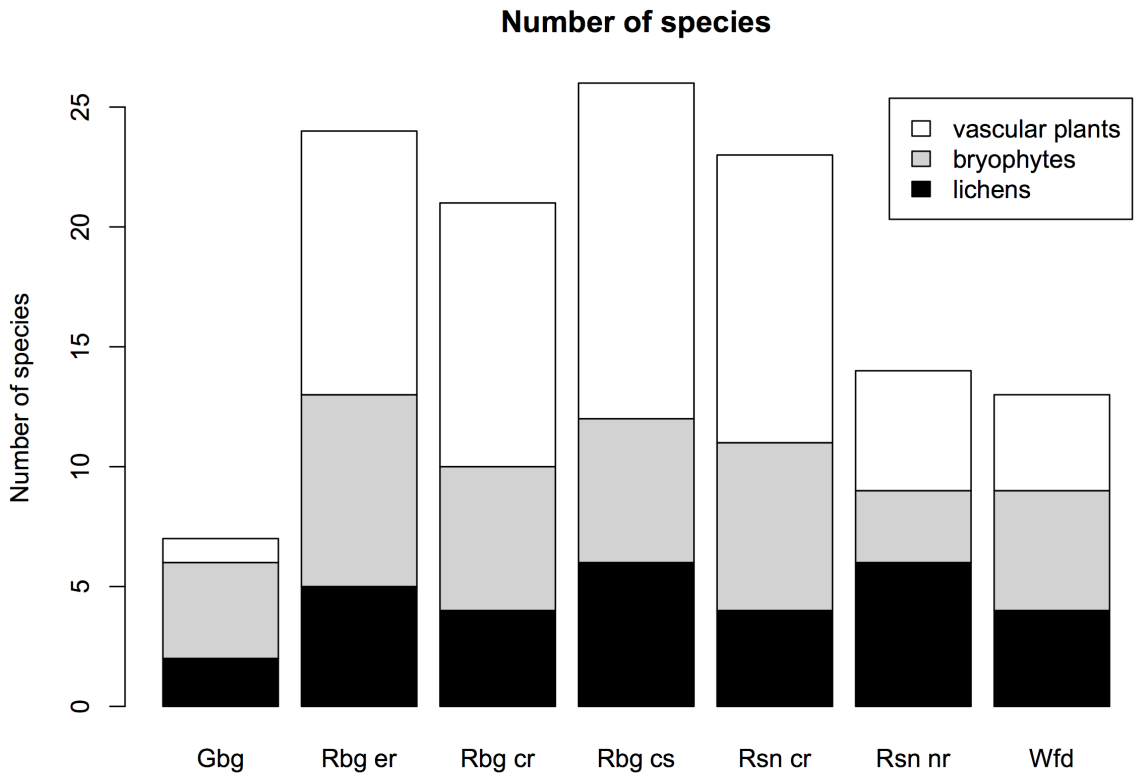

Figure 4: *Species richness at the investigated sampling sites. Refer to table 2 for an explanation of the abbreviations.*

Both, variables of wall chemistry as well as the new developed indices for wall heterogeneity are appropriate to differentiate the investigated castles according to their species composition (NMDS in figure 6). Both variable groups contribute a large fraction of explainable variation as revealed by variation partitioning using RDA with constrained predictors.
Vascular plants and bryophytes are more scattered in ordination space (their species composition is less uniform) and plots of the different castles are not separated (figure 6). Only a few environmental variables are explaining the pattern within these groups. Lichens seem to be most relevant for the distinction in the overall NMDS. Compared to the other groups, they depend more on structure and environment. The first axis of the NMDS analysis for the complete vegetation is correlating with the first axis of lichens (r: 0.73), the first axis of vascular plants (r: 0.65) and the first axis of bryophytes (r: 0.37). The second axis of all vegetation is correlated to the second axis of lichens (r: -0.48) and to the first axis of vascular plants (r: -0.42). Other correlations among axes showed an r below 0.2.

4. Discussion

If castle walls are differentiated based on their natural cover, then lichens are the species group of choice. Lichens are closer associated with building material than other species [2,9]. They are directly affected by moisture and chemical conditions such as pH [4,10,15,21]. Mosses and lichens adhere like a second skin to the castle wall surfaces. Often the first colonizers on monumental walls are lichens but differ on the different types of substratum they live on. Weber and Büdel [10] show that lichen species which where found on alkaline substratum like mortar are colonizing on the habitat faster than species on acidic substrate. Their growth is not dependent on grouts or cracks but their growth speed varies considerably between species [22]. Some lichen species with broad ecological amplitude, such as *Caloplaca citrina* or *Lecanora dispersa*, were found on all studied castles. The use of calcareous mortar explains the occurrence of calcicole lichens at Festung Rosenberg [see 4]. The mortar is soft and erodes much

faster than the stones. Thus the dilution of precipitation and the alkaline eroded material is preferred especially by fast establishing species like *Collema crispum*.

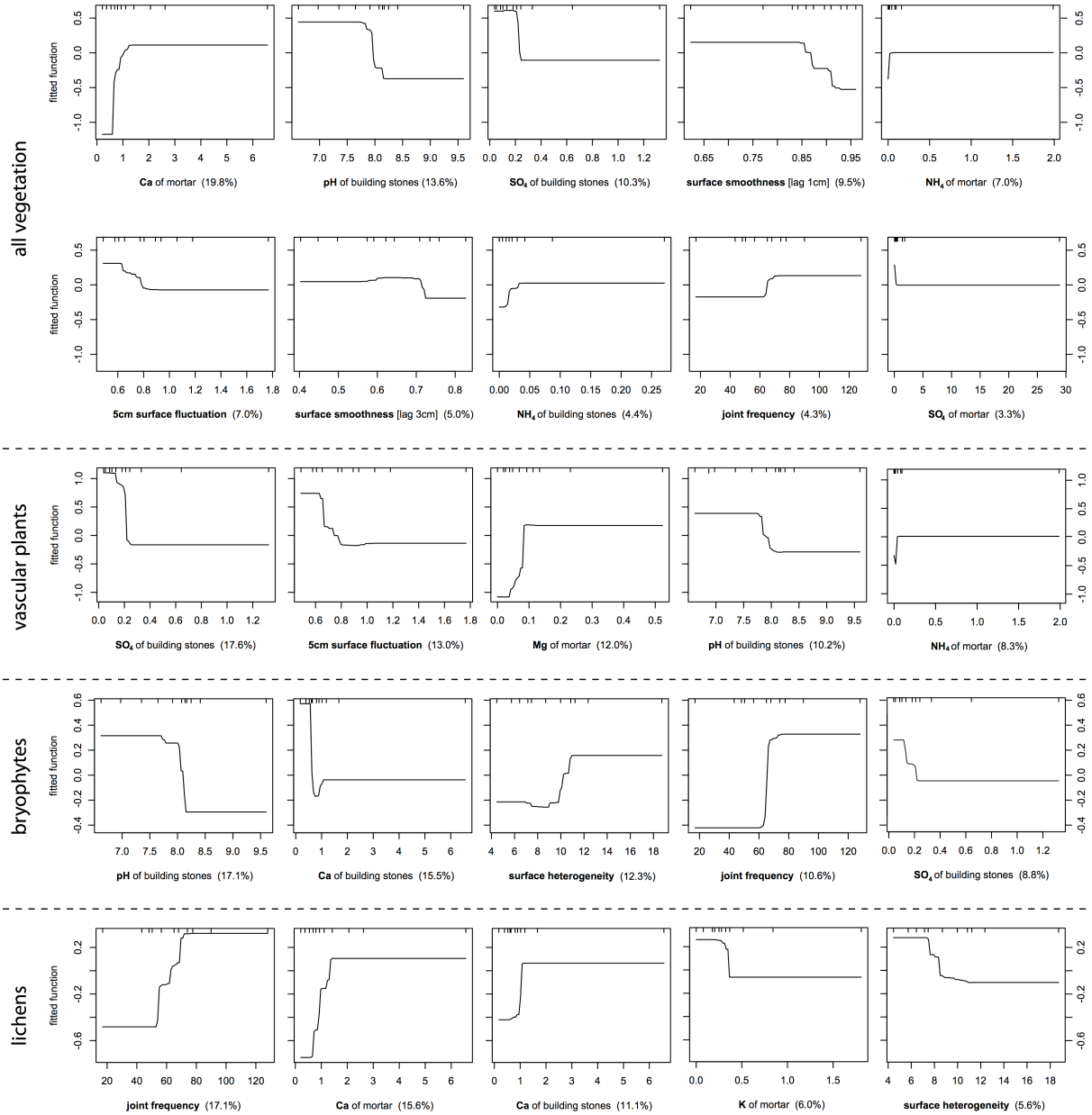

Figure 5: *Boosted regression trees for species richness (vascular plants + mosses + lichens). Percentages values in parentheses demonstrate the relative amount of predictive variation explained by these variables itself from the total variation. Rug plots inset at top of plots show distribution of sites across specific variable in deciles [18]. Soil variables tend to have large range of values without representation in the data set (no rug plot insets). These gaps should not be interpreted.*

Boosted regression tree results support a certain degree of interaction (namely competition) between mosses and lichens, which cannot be detected for vascular plants, but is also reported from other studies [23]. Mosses and lichens grow directly on the stone surface, which is not suitable for rooting vascular plants. In our study, species richness in lichens increases with calcium content of the stones, while the number of mosses decreases. Interestingly, an increase in calcium content of the mortar (not illustrated for lichens in figure 5) supports species richness in both groups.

Nitrate content is expected to have an effect on wall vegetation [8]. We find the ammonium content at Festung Rosenberg to be much higher than at other castles. The elevated values at the "environmental friendly" renovated part indicate that the originally used mortar or substrate in the open joints is still effective [compare 8]. Vascular plants are dependent on structures like joints or gaps where they can root mechanically and have access to a substrate that supports water and nutrients [5]. Thus, rough surfaces should host more species. In general this expectation is confirmed, but interesting cases were detected. Especially the decay in vascular plant richness with "5 cm surface fluctuations" (larger irregularities) was surprising. The negative relationship with "surface heterogeneity" indicates that "5 cm surface fluctuations" might be associated to building style with regular and thus less heterogenic stone arrangement having more alternations. "5 cm surface fluctuations" are especially low at Festung Rosenberg. Festung Rosenberg is, like parts of the Giechburg, build from sandstone. Stone arrangement is thus more regular than at the other castles. Festung Rosenberg is exceptional rich in vascular plants. Differentiating the effect of building stones and stone arrangement will need the extension of the study to further castles. There is hardly any difference in species composition between Festung Rosenberg and Burg Rabenstein. The building material has only little effect via the pH as plants will grow on calcium enriched mortar [8,2]. Species that prefer calcium rich habitats like *Asplenium ruta-muraria* are also growing at Festung Rosenberg as the mortar is produced from dolomite.

Even though there is no negative correlation between the number of lichen and moss species, the increase of mosses with "surface heterogeneity" and the decay of lichen species richness can be the result of competition between both groups. Moss species are probably not as good adapted to smooth surfaces than lichens, an instance that would be expected owing the tight spatial arrangement of lichen species on the wall surface.

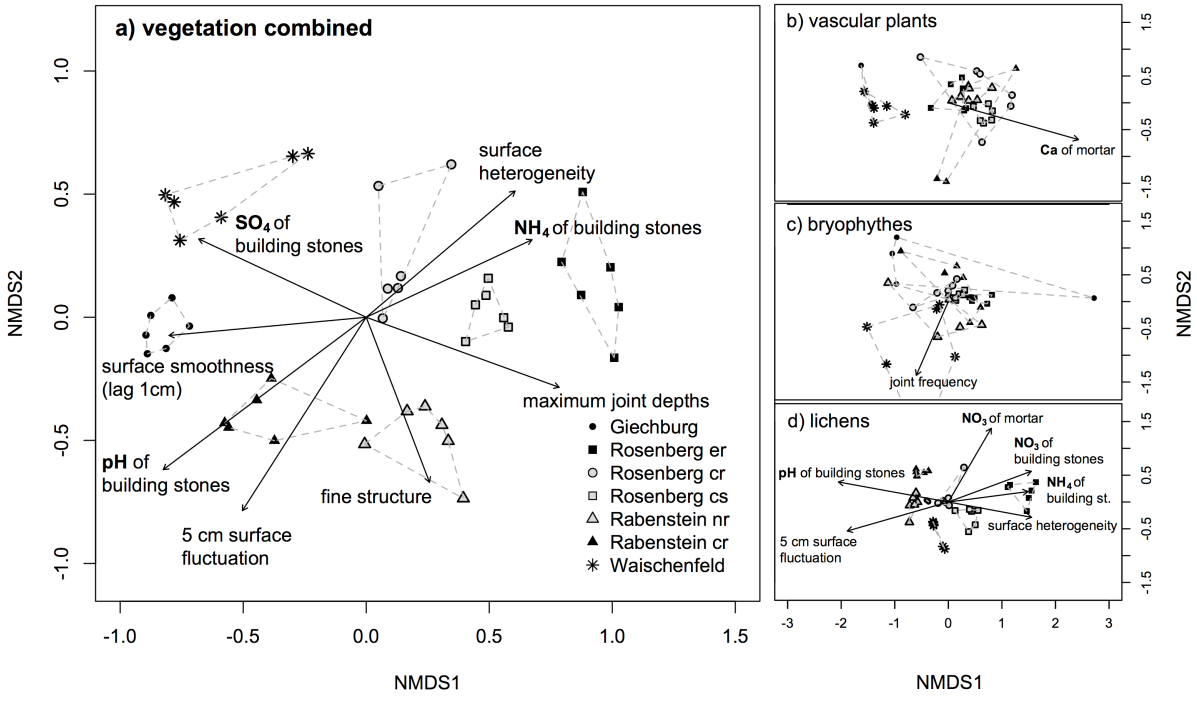

Figure 6: *Sampled walls are separated by an NMDS for all species groups (a). An analysis of vascular plants (b) and bryophythes (c) reveals much more scattered (dissimilar) species composition. The pattern for lichens indicates that this group is primarily responsible for the clear distinguishing of sampled walls in the analysis of all species groups combined. Environmental variables were fitted to the axis scores and tested on significance using permutation test. Only variables with p>0.01 are displayed.*

What can we learn for nature and monument restoration? It has been shown that the assumed "environmental friendly" restoration really results in different species composition. Depending on surface structure, building stones and (very important!) the chemistry of the used mortar, different species groups will be supported. This does not interfere with monument restoration goals. The assumption that wall vegetation is damaging historic buildings is still widely accepted [15,24,25,26] even if the contrary has already been suggested as early as 1911 [27]. In the 19th century wall vegetation has been named "green vandalism" [28]. Today's wording has changed to "biodeterioration" and a cleaning of the building from vegetation is arrogated [15,24,25]. In fact, the lateral growth of woody plants (roots and shoots) has the potential to break walls. However, the debate whether below ground parts of lichens, herbs and grasses do impose harmful pressure [15,29] or not [30] is still not finally settled. Detailed analyses of stone micro structure conducted at Festung Rosenberg by Drewello and Schmiedinger [31] have shown that neither higher plants (with the exception of woody plants) nor mosses accelerate biodeterioration of the sandstone. The vegetation has either none or a protective effect. The abundance of lichens may support a sealing of stone surfaces and prevents erosion. Constructive and biogenic induced carbonate accumulation underneath the surface of the sandstone has a deceleration effect on the corrosive degradation. Only the crustose lichen *Lecanora campestris* may cause permanent damages in singular cases at south facing walls at Festung Rosenberg. Granite churches in coastal Galicia indicate that lichen cover protects walls from salt induced disaggregation [32]. The authors propose a direct protection of the rock against salt or a decrease in the number of harmful wet-dry cycles by a balancing influence of lichens (also proposed by Honeyborne [30]). It has been shown that especially epilithic lichen species have protective effects on stone surfaces, where they reduce the deterioration of rainwater leaching [33] and thermal stress [34]. Moisture is a precondition for the establishment of wall vegetation [8]. As a positive feedback, vegetation is suspected to increase wall moisture by shielding the surface from insolation. However, this is not necessarily a problem as plant cover also prevents heat loss by radiation and decreases the number of harmful frost events [30]. However, hyphal penetration, expansion and contraction of lichen thalli within the rock are reported to have a severe deteriorating effect [35,36]. In addition, there is evidence for the chemical erosion potential of substances emitted from lichens [26,35,37]. It is thus still to be proven whether the erosion potential of lichens is minimal in comparison to abiotic erosion as suggested [26,30]. In general it is accepted that the effects of lichens are complex and vary in respect to species and substrate [15,38,39] and are in addition dependent on other environmental influences [40,41]. The effectiveness of restoration work is questioned by the speed of lichen recolonisation which may occur within few years [22,42,43,44]. Due to species-specific reactions, the successful use of herbicides is not guaranteed and regrowth is not prevented [44,45]. As species composition varies before and after recolonisation, it might be preferable to retain a more original and diverse communities on walls than to apply only short lasting restoration work [44]. Novel methods of lichen identification and assessments of their specific effects are currently developed [39,46,47] and may support decision makers in choosing the right treatment for a conservation of old stone surfaces on historic monuments [48,49]. An inconsiderate removal of vegetation is, with the exception of woody plants, questionable for monument restoration. In fact, preventive methods need to be designed case specific [36,39] as it is possible that the removing of flora (esp. lichens) could accelerate the erosion of rock surfaces [50]. An effective cleaning would alter the wall surface and is aligned with a considerable loss of material while being non sustainable [31,39,51]. Mechanical removal strategies are in addition ineffective for endolithic lichens and might even have a reverse effect in case of asexually reproducing species [52]. Biochemical treatments, however, might have negative effect on environment and health but are steadily improved [46,47]. Meanwhile a multitude of different mechanical, physical and chemical methods as well as bioremediation techniques have been developed to handle biodeteriogens [53]. Successful are methods combining mechanical and chemical approaches [53]. However, often the positive (preservative) effects of the lichens on the substratum prevail possible negative effects [51,54]. Thus both, nature conservation and monument

conservation goals can be achieved by a selective case specific evaluation whether a treatment is necessary and which one is most effective [39,51].
The type of habitat that is provided by historic monuments has become rare in the European cultural landscape. But despite this value for nature preservation, the specific vegetation of walls is also of cultural and historic importance. A large fraction of the plants still growing near castles have already been used in the medieval times for food or healing [55]. Others had a more ornamental or even magic purpose. In many cases knowledge on the original use has been lost. Notwithstanding wall vegetation has characterised the historic picture of monasteries, churches, city walls and castles for centuries and their conservation is thus also in the interest of historic conservation [55].
Spreading random plots on the same castle walls does not result in true repetitions. The resulting plots are spatially autocorrelated and violate the assumption of independence. The aggregated arrangement of the plots belonging to one castle in the NMDS results shows the similarity between plots belonging to one castle. Out of practical reasons a statistically perfect sampling design is often not feasible. An independent distribution of several plots per castle wall is a compromise that is not uncommon in praxis [56]. Extending the study to further locations would enhance statistical certainty, but is costly in terms of time and money. The chosen schematic approach is replicable and results are can easier be compared and transferred than subjective assessments.

5. Conclusion

The indices used to characterise the wall structure where developed based on theoretical considerations. The aim was to gain meaningful values that could be associated to species richness and composition on the wall. The indices should mirror the characteristic surface settings of the investigated walls. Until today, no other investigation of historic buildings has included wall structure in such detail. It has been shown that heterogeneity on walls (or other surfaces) can be assessed in a representative way not only qualitatively but also quantitatively. This novel approach enabled us to relate surface heterogeneity of walls to the associated vegetation. However, surface heterogeneity is also interacting with cleaning methods [36]. An extension of the methodology from a 2D line measurement to a 3D surface assessment might (e.g. via laser scanning) be a feasible (albeit expensive) task for future studies in this direction. A theoretical baseline for this approach has been provided here.

References

[1] E. Pacini, Purposes and manners of representation of plants in the European art of 13th-17th century. Pact Journal 42 (1994), 172-180.
[2] O. Gilbert, Rooted in stone. The natural flora of urban walls, English Nature, Peterborough, 1992.
[3] R. Pick, S. Beyer, R. Drewello, D. Förster, A.S. Laber, M. Rauh, A. Schmiedinger, R. Weißmann, Denkmalpflege und Ökologie - Instandhaltung von ökologisch bedeutsamem Mauerwerk am Beispiel der Wallmauern der Festung Rosenberg in Kronach. Bayerisches Landesamt für Denkmalpflege, München, 2002.
[4] B. Prieto, T. Rivas, B. Silva, Environmental factors affecting the distribution of lichens on granitic monuments in the Iberian peninsula. The Lichenologist 31 (1999), 291-305.
[5] M. Duchoslav, Flora and vegetation of stony walls in East Bohemia. Preslia 74 (2002), 1-25.
[6] A. Darlington, Ecology of walls - Heinemann Educational Books, London, 1981.
[7] B. Leutner, M.J. Steinbauer, C.M. Müller, A.J. Früh, S. Irl, A. Jentsch, C. Beierkuhnlein, Mosses like it rough - growth form specific responses of mosses, herbaceous and woody plants to micro-relief heterogeneity. Diversity 4 (2012) 59-73.
[8] W. Werner, M. Gödde, N. Grimbach, Vegetation der Mauerfugen am Niederrhein und ihre Standortverhältnisse. Tuexenia 9 (1989), 57-73.
[9] S. Segal, Notes on wall vegetation. Dr. W. Junk N. V., The Hague, Netherlands, 1969.
[10] B. Weber, B. Büdel, Mapping and analysis of distribution patterns of lichens on rural medieval churches in north-eastern Germany. Lichenologist 33 (2001), 231-248.
[11] A.M. Bellinzoni, G. Caneva, S. Ricci, Ecological trends in travertine colonisation by pioneer algae and plant communities. International Biodeterioration and Biodegradation 51 (2003), 203-210.
[12] E. Oberdorfer, Pflanzensoziologische Exkursionsflora. Ulmer-Verlag, Stuttgart, 1990.
[13] J.P. Frahm, W. Frey, Moosflora. Ulmer-Verlag, Stuttgart, 1992.
[14] V. Wirth, Die Flechten Baden-Württembergs. Ulmer-Verlag, Stuttgart, 1995.

[15] M. Lisci, M. Monte, E. Pacini, Lichens and higher plants on stone: a review. International Biodeterioration and Biodegradation 51 (2003), 1-17.
[16] G. Pavlidis, A. Koutsoudis, F. Arnaoutoglou, V. Tsioukas, C. Chamzas, Methods for 3Ddigitization of cultural heritage. Journal of Cultural Heritage 8 (2007), 93-98.
[17] R Development Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, 2009.
[18] J. Elith, J.R. Leathwick, T. Hastie, A working guide to boosted regression trees. Journal of animal ecology 77 (2008), 802-813.
[19] B. McCune, J. Grace, Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon, 2002.
[20] J. Oksanen, F.G. Blanchet, R. Kindt, P. Legendre, R.G. O'Hara, G. Simpson, P. Solymos, M.H. Stevens, H. Wagner, vegan: Community Ecology Package. R package version 1.17-0, 2010.
[21] L.B. Sparrius, A. Aptroot, K.V. Herk, Diversity and ecology of lichens on churches in the Netherlands. Nova Hedwigia 85 (2007), 299-316.
[22] S.E. Favero-Longo, A. Borghi, M. Tretiach, R. Piervittori, In vitro receptivity of carbonate rocks to endolithic lichen-forming aposymbionts. Mycological Research 113 (2009), 1216–1227.
[23] S.E. Favero-Longo, R. Piervittori, Lichen-plant interactions. Journal of Plant Interactions 5 (2010), 163-177.
[24] A.K. Mishra, K.K. Jain, K.L. Garg, Role of higher plants in the deterioration of historic buildings. Science of The Total Environment 167 (1995), 375-392.
[25] C.H. Lee, J.E. Yi, Weathering damage evaluation of rock properties in the Bunhwangsa temple stone pagoda, Gyeongju, Republic of Korea. Environmental geology 52 (2007), 1193-1205.
[26] A. Cicek, A. Aslan, K. Yazici, A.S. Koparal, Effects of environmental conditions on historical buildings: lichens and NOx gases. Environmental monitoring and assessment 154 (2009), 187-195.
[27] J. Watson, British and Foreign Building Stones. CUP, Cambridge, 1911.
[28] J. Scheiger, Von dem Einflusse der Pflanzen auf die Zerstörung der Ruinen. Berichte und Mitteilungen des Alertums-Vereines zu Wien 2 (1857), 1-6.
[29] S.E. Favero-Longo, C. Gazzano, M. Girlanda, D. Castelli, M. Tretiach, C. Baiocchi, R. Piervittori, Physical and chemical deterioration of silicate and carbonate rocks by meristematic microcolonial fungi and endolithic lichens (chaetothyriomycetidae). Geomicrobiology Journal 28 (2011), 732–744.
[30] D.B. Honeyborne, Weathering and decay of masonry. In: J. Ashurst, F.G. Dimes (Eds.), Conservation of building and decorative stone: part 1 (2nd ed.), Butterworth-Heinemann, Oxford, 1998.
[31] R. Drewello, A. Schmiedinger, The sandstone of the fortess Rosenberg in Kronach - between ecology and cultural heritage preservation. Zeitschrift der deutschen Gesellschaft für Geowissenschaften 158 (2007), 895-919.
[32] R. Carballal, G. Paz-Bermúdez, M.J. Sánchez-Biezma, B. Prieto, Lichen colonization of coastal churches in Galicia: biodeterioration implications. International Biodeterioration and Biodegradation 47 (2001), 157-163.
[33] D. Mottershead, G. Lucas, The role of lichens in inhibiting erosion of a soluble rock. Lichenologist 32 (2000), 601-609.
[34] N.E.A. Carter, H.A. Viles, Experimental investigations into the interactions between moisture, rock surface temperatures and an epilithic lichen cover in the bioprotection of lichen. Building and Environment 38 (2003), 1225–1234.
[35] J. Chen, H.P. Blume, L. Beyer, Weathering of rocks induced by lichen colonization – a review. Catena 39 (2000), 121–146.
[36] B. Cámara, A. De los Ríos, M. Urizal, M. Álvarez de Buergo, M.J. Varas, R. Fort, C. Ascaso, Characterizing the microbial colonization of a dolostone quarry: Implications for stone biodeterioration and response to biocide treatments. Microbial Ecology 62 (2011), 299-313.
[37] P. Adamo, P. Violante, Weathering of rocks and neogenesis of minerals associated with lichen activity. Applied Clay Science 16 (2000), 229–256.
[38] S.E. Favero-Longo, D. Castelli, O. Salvadori, E. Belluso, R. Piervittori, Pedogenetic action of the lichens *Lecidea atrobrunnea, Rhizocarpon geographicum* gr. and *Sporastatia testudinea* on serpentinized ultramafic rocks in an alpine environment. International Biodeterioration and Biodegradation 56 (2005), 17–27.
[39] R. Piervittori, S.E. Favero-Longo, C. Gazzano, Lichens and biodeterioration of stonework: A review. Chimica Oggi 27 (2009), 8-11.
[40] N.E.A. Carter, H.A. Viles, Bioprotection explored: the story of a little known earth surface process. Geomorphology 67 (2005), 273-281.
[41] V. Sousa, N. Almeida, I. Meireles, J. de Brito, Anomalies in wall renders: overview of the main causes of degradation. International Journal of Architectural Heritage 5 (2011), 198–218.
[42] B. Silva, B. Prieto, T. Rivas, M.J. Sanchez-Biezma, G. Paz, R. Carballal, Rapid Biological Colonization of a granitic building by lichens. International Biodeterioration and Biodegradation 40 (1997), 263-267.
[43] J. Nascimbene, O. Salvadori, Lichen recolonization on restored calcareous statues of three Venetian villas. International Biodeterioration and Biodegradation 62 (2008), 313-318.
[44] J. Nascimbene, O. Salvadori, P.L. Nimis, Monitoring lichen recolonization on a restored calcareous statue. Science of The Total Environment 407 (2009), 2420-2426.

[45] T. Mouga, M. Almeida, Neutralisation of herbicides - Effects on wall vegetation. International Biodeterioration and Biodegradation 40 (1997), 141-149.
[46] A.J. Fonseca, F. Pina, M.F. Macedo, N. Leal, A. Romanowska-Deskins, L. Laiz, A. Gómez-Bolea, C. Saiz-Jimenez, Anatase as an alternative application for preventing biodeterioration of mortars: Evaluation and comparison with other biocideses. International Biodeterioration and Biodegradation 64 (2010), 388-396.
[47] M.F. Gazulla, E. Sánchez, J.M. González, M.C. Portillo, M. Orduña, Relationship between certain ceramic roofing tile characteristics and biodeterioration. Journal of the European Ceramic Society 31 (2011), 2753–2761.
[48] C. Gazzano, S.E. Favero-Longo, E. Matteucci, R. Piervittori, Image analysis for measuring lichen colonization on and within stonework. The Lichenologist 41 (2009), 299–313.
[49] C. Gazzano, S.E. Favero-Longo, E. Matteucci, A. Roccardi, R. Piervittori, Index of Lichen Potential Biodeteriogenic Activity (LPBA): A tentative tool to evaluate the lichen impact on stonework. International Biodeterioration and Biodegradation 63 (2009), 836-843.
[50] Mycological Research News, Mycological Research 105 (2001), 385-386.
[51] C. Beierkuhnlein, R. Drewello, R. Snethlage, L. Töpfer, (eds.), Zwischen Denkmalschutz und Naturschutz, Initiativen zum Naturschutz 83, Erich Schmidt Verlag, Berlin, 2011.
[52] G. Caneva, M.P. Nugari, D. Pinna, Il controllo del degrado biologico, Nardini Editore, Fiesole, Italy, pp. 3-200, 1996.
[53] G. Caneva, M.P. Nugari, O. Salvadori, Plant Biology for Cultural Heritage: Biodeterioration and Conservation. Los Angeles: Getty Conservation Institute, 2009.
[54] A.S. Hygen, Protection of Rock Art: The Rock Art Project 1996–2005; Final Report from the Directorate for Cultural Heritage. Oslo: Directorate for Cultural Heritage Archive.
[55] K. Dehnen-Schmutz, Alien species reflecting history: medieval castles in Germany. Diversity and Distributions 10 (2004), 147-151.
[56] J. Leps, P. Smilauer, Multivariate analysis of ecological data using CANOCO. University Press, Cambridge, 2003.
[57] Bayerisches Landesamt für Umwelt, 2007. Naturräumliche Gliederung Bayerns, online at http://www.lfu.bayern.de/natur/daten/naturraeume/index.htm, 02.07.2008.
[58] H. Kunstmann, Die Burgen der östlichen fränkischen Schweiz. Kommissionsverlag Ferdinand Schöningh, Würzburg, 1965.
[59] T. Eckert, S. Fischer, R. Freitag, R. Hofmann, W. Tausendpfund, Die Burgen der Fränkischen Schweiz. Ein Kulturführer, Gebietsausschuß Fränkische Schweiz, Forchheim, 1992.
[60] E. Walter, 1000-Jähriges Kronach- Stadt und Umgebung. Heimatbeilage zum Oberfränkischen Schulanzeiger, Nr. 308, Bayreuth, 2003.
[61] H. Kremer, Führer durch die Festung Rosenberg ob Kronach. Carl Link Verlag, Kronach, 1974.

8. Manuscript 7 - Mosses Like It Rough - Growth Form Specific Responses of Mosses, Herbaceous and Woody Plants to Micro-Relief Heterogeneity

Diversity 4 (2012) DOI:10.3390/d40x000x

Benjamin F. Leutner [1,2], Manuel J. Steinbauer [1,*], Carina M. Müller [1], Andrea J. Früh [1], Severin Irl [1,3], Anke Jentsch [3] and Carl Beierkuhnlein [1]

[1]Biogeography, BayCEER, University of Bayreuth, Bayreuth 95440, Germany;
E-Mails: b.leutner@gmx.de (B.F.L.); Carina.M.Mueller@web.de (C.M.M.);
frueh.andrea@googlemail.com (A.J.F.); severin.irl@uni-bayreuth.de (S.I.);
carl.beierkuhnlein@uni-bayreuth.de (C.B.)
[2]Biogeographical Modelling, BayCEER, University of Bayreuth, Bayreuth 95440, Germany
[3]Disturbance Ecology, BayCEER, University of Bayreuth, Bayreuth 95440, Germany;
E-Mail: anke.jentsch@uni-bayreuth.de
* Author to whom correspondence should be addressed; E-Mail: manuel.steinbauer@uni-bayreuth.de; Tel.: +49-921-55-2211; Fax: +49-921-55-2315.

Abstract: Micro-relief heterogeneity can lead to substantial variability in microclimate and hence niche opportunities on a small scale. We explored the relationship between plant species richness and small-scale heterogeneity of micro-relief on the subtropical island of La Palma, Canary Islands. Overall, we sampled 40 plots in laurel and pine forests at four altitudinal bands. Species richness was recorded separately for various growth forms (*i.e.*, mosses, herbaceous and woody plants). Site conditions such as altitude, slope, aspect, and tree density were measured. Micro-relief heterogeneity was characterized by surface structure and a subsequently derived surface heterogeneity index. The effect of micro-relief heterogeneity on species richness was analysed by means of linear mixed effect models and variance partitioning. Effects of micro-relief heterogeneity on species richness varied considerably between growth forms. While moss richness was affected significantly by micro-relief heterogeneity, herbaceous and woody plants richness responded mainly to larger-scale site conditions such as aspect and tree density. Our results stress the importance of small-scale relief heterogeneity for the explanation of spatial patterns of species richness. This poses new challenges as small-scale heterogeneity is largely underrepresented, e.g. with regard to its application in species distribution models.

Keywords: biodiversity; habitat heterogeneity; micro-topography; topographic variability; northernness; species diversity; Bitterlich; altitudinal gradient; laurel forest; climate change

1. Introduction

Projections on future developments based on current species distribution models reveal substantial elevational shifts of occurrences of plant species under climate change [1,2]. This could drive many species - unable to reach climatically suitable habitats - to the brink of extinction [3]. However, these models do not include small-scale differences in relief-heterogeneity [4]. Scherrer and Körner [5] highlighted the role of thermal differences on the metre-scale in alpine ecosystems that even exceed the IPCC temperature projections for the end of this century [6]. A mosaic of microclimatic conditions could thus create refuges and stepping stones in a warmer climate within just a few metres distance from the previous location of a plant population [7]. This implies that according to the niche theory [8], more species should be found in heterogeneous environments compared to homogenous environments, because more spatial and ecological niches are available. A positive correlation has been found between topographic variability, site heterogeneity and species richness, e.g. [9-11]. Nevertheless in a recent review Lundholm [12] showed that the relationship between plant species richness and environmental heterogeneity is not that straightforward as even negative relationships have been reported. The relationship seems to be most pronounced in communities with medium productivity [13]. Relief heterogeneity is an important factor regulating soil moisture [14], microclimate [7] and plant available nutrients [15,16]. Also the intensity of stress (e.g. soil erosion or thickness of a poorly decomposable litter layer) is influenced by relief heterogeneity [17]. Habitats that incorporate a heterogeneous relief, provide a greater number of ecological niches and thus can be expected to host a highly diverse species composition [18]. This is confirmed at the micro- and meso-scale [12]. Competitive exclusion is reduced in heterogeneous environments as they provide more diverging abiotic conditions for growth or vary stronger in their disturbance frequency or magnitude [19,20]. In addition, small-scale genetic differentiation in plants occurs commonly within micro-environmental heterogeneity, at small spatial scales [21]. As plants differ in their ability to respond to small-scale variability in abiotic conditions, it is assumed that mosses and herbaceous plants can profit more by micro-relief heterogeneity compared to trees and bushes [22].

In ecological studies, especially when it comes to theory, relief heterogeneity is integrated with environmental and biotic heterogeneity. Terminology is often imprecise using "habitat heterogeneity" [23] or "complexity" [24,25] interchangeably. While this may be justified in theoretical concepts, more specific approaches are required in empirical studies. In addition, relief heterogeneity is mostly detected via rather general and simplistic variables such as elevation, slope or aspect [15].

To date, studies that address the effect of relief heterogeneity on species richness focused on regional to landscape scales (*i.e.*, with a grain often much larger than one km^2, e.g. [26]), although Hofer *et al.* [10] demonstrated that small-scale topographic variability (25 m scale) can be one of the major explanatory variables of species richness in gradient dominated landscapes and is predicted to become even more important in a prospective warmer climate [7]. Moreover, it has not been tested whether this relationship is modified by elevation. Studies that apply a fine spatial grain are missing, and the challenges and knowledge gaps especially at this scale are limiting the quality of climatic envelope approaches. Most likely this is due to the fact that at this scale spatial heterogeneity has to be measured and cannot be derived from existing geo-information such as topography.

To investigate the linkage of micro-relief and species richness we conducted a vegetation survey on La Palma, Canary Islands. This island is well suited for this purpose as it offers a large plant species pool [27] as well as a wide altitudinal range [28]. We focused on forested areas, as these provide continuous natural vegetation along the altitudinal gradient. Non-forested ecosystems in contrast are restricted to the subalpine mountain peaks and the lower altitudes.

The first hypothesis tested in this study is that small-scale micro-relief heterogeneity positively affects species richness. The supporting effect of micro-relief heterogeneity on species richness is expected to be stronger in higher altitudinal bands compared to lower ones as relief hetero-

geneity has been suggested to increase with altitude [10]. Additionally, in the increasingly harsh environments of high altitudes plants would profit more from the availability of micro-climatic refuges. Our second hypothesis refers to plant growth forms. Species richness of mosses and herbaceous plants are hypothesised to be influenced more strongly by small-scale micro-relief heterogeneity than the richness of woody species (see also [22]).

2. Background and Methods

2.1. Study Area

The study site is located on the volcanic Island of La Palma, Canary Island archipelago, Spain (28°54'N; 17°50'W). La Palma comprises an area of approximately 700 km^2 and rises from sea level to 2423 m.a.s.l., thus, resulting in very steep slopes. The island is characterized by a strong NE-SW gradient in rainfall and water availability with a strongly contrasting altitudinal zonation mainly due to a thermic inversion and the topographic barrier effect of the mountains. Ascending humid air masses of the trade-winds (NE winds) frequently form a stratocumulus layer in altitudes ranging from 800 m up to the seasonally varying thermal inversion at 1000 to 1500 m [29,30]. This climatic setting supports a distinct vegetation zonation from semi-arid succulent shrub to evergreen laurel forests, pine forests and subalpine shrub vegetation [31].

The two prevailing natural forest types incorporated in this study were laurel and pine forest. The former is limited to humid conditions with precipitation provided by the stratocumulus layer and extends from 500 to 1200 m. The laurel forest is concentrated on the NE-facing slopes. It comprises about 20 tree species, which form a dense canopy, leading to low light availability within the stand and a moderate understorey consisting of shrubs, herbs, ferns and moss species. Characteristic evergreen broadleaved woody species (nomenclature following [32]) are *Apollonias barbujana* (Cav.) Bornm., *Laurus novocanariensis* Rivas-Mart., Lousa, Prieto, Días, Costa and Aguiar, *Ocotea foetens* (Aiton.) Baill., *Persea indica* (L.) Spreng., *Morella faya* (Aiton) Wilbur, *Viburnum rigidum* Vent., *Ilex canariensis* Poir., *Sonchus palmensis* (Sch. Bip.) Boulos, and *Hedera canariensis* Willd.

The pine forest is dominated by one tree species; the Canary endemic *Pinus canariensis* Sweet ex Spreng. Although the forest structure is more open than the laurel forest and much light is available, the abundance of the understorey vegetation is low and a thick layer of needle litter covers the ground. Common understorey species are *Cistus symphytifolius* Lam., *Pteridium aquilinum* (L.) Kuhn in Kerst., *Adenocarpus foliolosus* (Aiton) DC., and *A. viscosus* ssp. *spartioides* (Willd.) Webb and Berthel. Pine forests occur between 1200 to 2100 m and are repeatedly subject to natural but also anthropogenic fires.

2.2. Sampling Design

The sampled sites were located on the northeastern slopes of La Palma. Sampling took place in April 2011. We sampled in four altitudinal bands (550, 750, 1450, and 1600 m.a.s.l.) allowing for an altitudinal range of +/- 50 m in each band depending on local accessibility. Within each altitudinal band 10 plots were sampled.

For every altitudinal band a point of origin was fixed from which we walked in random directions determined by a random number generator. We stopped when all predefined suitability criteria were met in order to ensure the comparability between plots. Plots were considered suitable if slopes were shallower than 25°, had, a minimum distance of 5 m to tracks as well as 30 m between the plots.

We used rectangular plots (5 × 8 m) oriented parallel to the slope. For each plot GPS coordinates, aspect, altitude, and slope of the two downhill facing sides of the plot (β in Figure 1) were recorded. We used the Bitterlich-stick method (0.5 cm angle; 50 cm stick), a measure of basal area (see e.g. [33]) to obtain an index of tree density. All plant species within the plot were recorded and classified to the basic growth forms: mosses, herbaceous (including herbs, grasses and ferns) and woody plants (including shrubs and trees).

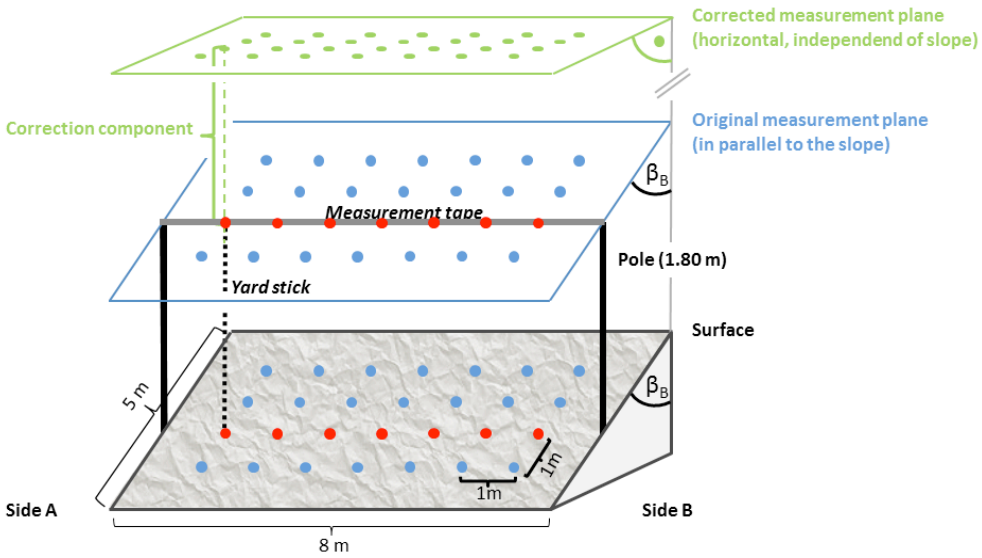

Figure 1. *Within-plot sampling design: four transects of seven measurements each, resulting in 22 regular measurements (blue dots). Original sampling was performed from an imaginary plane 1.80 m above the plot and parallel to the slope. Values were corrected to equal those, which would have been obtained if they had been measured from a horizontal plane (green dots). Red dots emphasize the measurements of one transect.*

2.3. Micro Relief Heterogeneity

We aimed to develop a rapid and repeatable technique suitable for assessment of micro relief heterogeneity in the field. As the very dense understorey prevented application of the classical chain method [34] or theodolite measurements, the deviance of the relief from a plane surface was measured.

For the measurement of deviance, the micro-relief elevations within the plot were measured along four transects parallel to the slope (see Figure 1). For each transect we spanned a scaled tape in 1.80 m height and measured the perpendicular distance to the surface using a yardstick at every metre. Transects were spaced in one metre distances in order to achieve a regular grid of four times seven measurements.

The measured perpendicular distance values were corrected for the slope in order to ensure that directional effects of heterogeneity would not be lost due to the way of measuring only parallel to the slope. Therefore, the angles in the slope direction were used to calculate the required offset correction component (Equation 1). Since the angles could differ on the two sides of the plot they were both included with a weighting factor, which decreased linearly with distance of the measured point to the respective side of the plot, *i.e.*, a weighted average:

$$h_{corrected} = h_{old} + w_A * \sin(\beta_A) * d + w_B * \sin(\beta_B) * d \quad (1)$$

with h_{old} being the measured height, w being the weighting factors, β being the slope angle, d the distance of the transect from the origin and subscript A being the left side of the plot and B the right side, respectively. The weighting factors are w_A = {1; 5/6; …; 0| for A → B} and vice versa for w_B. The slope parallel angles were small, *i.e.*, smaller than 6°, and hence neglected. The resulting corrected values correspond to hypothetical measurements from a horizontal plane (Figure 1).

Based on artificially created test surfaces, e.g. very smooth surfaces *vs.* very rough surfaces, we developed the following set of heterogeneity indices: "Index 1" was calculated based on a moving window which encompassed four measurement points and was shifted across the relief data. For each window the standard deviation of the contained points was calculated. Subsequently, the standard deviations of all windows were averaged. For "Index 2" the standard deviation of each measurement transect was calculated and averaged across the four transects.

"Index 3" was the elevational range between total minimum and total maximum of all measured points. Finally, "Index 4" was calculated as the sum of the Euclidean distances between successive pairs of measurement points within each transect, that were eventually summed over all transects.

Initial testing of the four statistical indices of relief heterogeneity on a set of artificial test surfaces (Figure 2) revealed two suitable indices. Both "Index 1" based on moving window standard deviations and "Index 4" representing the total transect-wise surface length, achieved the desired property of increasing values with increasing degree of small-scale heterogeneity (Figure 3). "Index 2" and "Index 3" were not sensitive to changes in small-scale heterogeneity and hence discarded. Since "Index 1" and "Index 4" were highly correlated (Pearson correlation coefficient = 0.97) all further analyses were restricted to using "Index 1" only. Statistical measures similar to "Index 1" to quantify topographic variability on various scales based on digital elevation models have been used and tested frequently before (e.g. [35–38]). Note that there is collinearity between small-scale heterogeneity and surface area that cannot be disentangled [39].

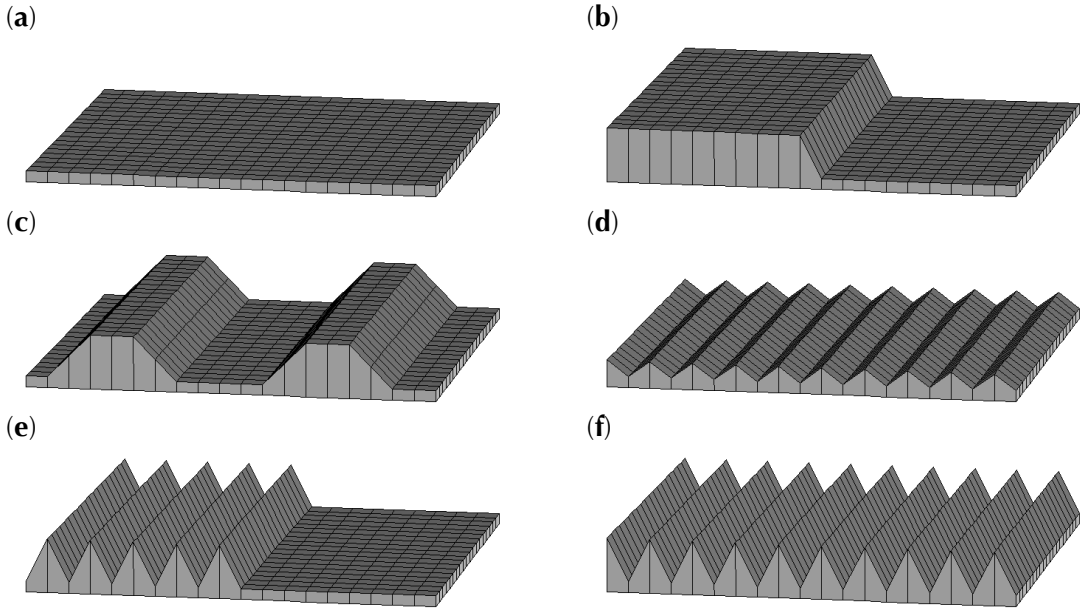

Figure 2. *Artificial test surfaces, which were used to select sensitive indices of small-scale microrelief heterogeneity: (**a**) perfectly smooth surface; (**b**) perfectly smooth surface with one step of 0.8 m; (**c**) mixture of perfectly smooth surface and two big humps (range 0.8 m); (**d**) rough surface (range: 0.3 m); (**e**) even mixture of perfectly smooth and very rough surface (range 0.8 m); (**f**) very rough surface (range: 0.8 m).*

As the values of aspect are circular (0–360°), we calculated the cosine of all aspects to retrieve the non-circular variable "northernness" (1 = North … 0 = East … −1 = South). Since all our plots were facing east we did not need to consider the corresponding "easternness".

2.4. Analysis

In order to analyse the effect of small-scale heterogeneity we fitted linear mixed effect models for the response variables species number of mosses, herbaceous and woody plants and their sum, the total species richness, respectively. We applied the *lme* function from the nlme R package v.3.1-100 [40]. Micro-relief heterogeneity, tree density and northernness were included as fixed factors, the altitudinal band as a random factor (Equation 2). For model fitting the restricted maximum log-likelihood was maximized. In order to test whether the vegetation type, namely laurel or pine forest, exhibited a significant confounding influence on our results, we fitted the same mixed effect models using the *lmer* function of the lme4 R package v.0.999375-42 [41], since the *lme* function does not allow for crossed random effects. Using AIC and χ^2 test p-values of an *ANOVA* we then compared the models with altitudinal band as random factor with those constructed including both altitudinal band and vegetation type as random factors. Based on the same test criteria we conducted a stepwise forward model selection to test, which fixed and random factors resulted in the best model fit. The residuals were tested for normality using the Shapiro-Wilk's test as well as qq-plots. Where residuals were not normally distributed, which was the case for herbaceous and woody plants, the response variable was log-transformed resulting in normal distribution of the residuals. In order to evaluate the importance of small-scale heterogeneity for species richness in the different altitudinal bands, we applied variance partitioning on all response variables by means of the function *varpart* in the vegan package v.1.17-10 [42]. We did so for each altitudinal band separately. The explanatory variables for the linear model were micro-relief heterogeneity, tree density and northernness. Furthermore, we calculated the variance partitioning over all altitudinal bands by combining northernness and altitudinal band into one explanatory group. We report the proportion of explained variance calculated as adjusted R^2. For R^2 values close to zero the calculation of the adjusted R^2 can occasionally result in negative values. Following Legendre [43] these are artefacts and are to be interpreted as zero explained variance. All data were analysed using R 2.13.0 [44].

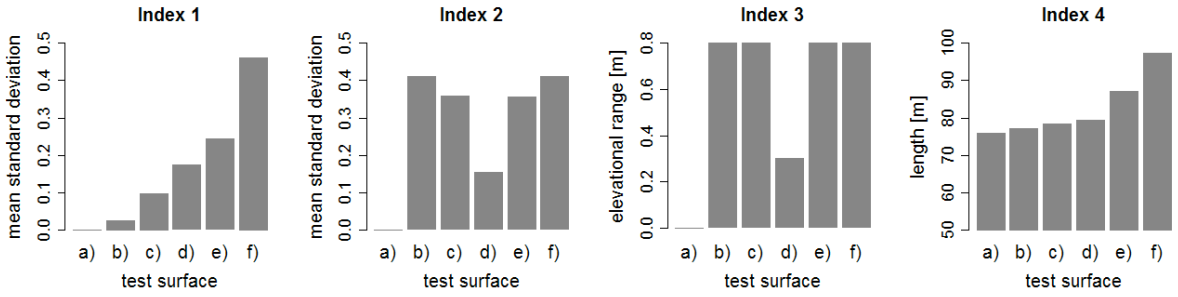

Figure 3. *Performance of different indices of relief heterogeneity on the test-surfaces presented in Figure 2. "Index 1": Mean four point moving window standard deviation. "Index 2": Mean transect wise standard deviation. "Index 3": range of all measured elevations. "Index 4": transect wise length.*

3. Results

The number of plant species per plot varied from 3 to 18. Species richness within the four altitudinal bands was highly variable. However, differences between these bands were only significant between the lower pine forest and the laurel forest bands with the latter having a higher species richness (Figure 4, Tukey HSD, $p < 0.05$).

Among all collected parameters in the field study micro-relief heterogeneity, tree density and northernness were revealed as the best predictors in the linear mixed-effect model for total species richness. Total species richness was significantly affected by micro-relief heterogeneity, tree density and northernness (Table 1). However, the proportion of variance explained by micro-relief heterogeneity was relatively low (10%) compared to tree density (20%) and 'altitudinal band and northernness' (34%; combined to one variable) (Figure 5).

Linear mixed-effect models revealed different responses of growth forms to the explanatory variables (Table 1). Species richness of mosses was positively influenced by micro-relief heterogeneity. In contrast, tree density and northernness were both non-significant (Table 1). Herbaceous species richness showed no significant relationship to micro-relief heterogeneity, unlike the significant determinants tree density (regression estimator: −0.064 ± 0.009, log-transformed) and northernness (regression estimator: 0.249 ± 0.072, log-transformed). The same applied to woody plants, which showed no significant response to micro-relief heterogeneity but significant responses to tree density (regression estimator: −0.023 ± 0.007, log-transformed) and northernness (regression estimator: 0.111 ± 0.049, log-transformed).

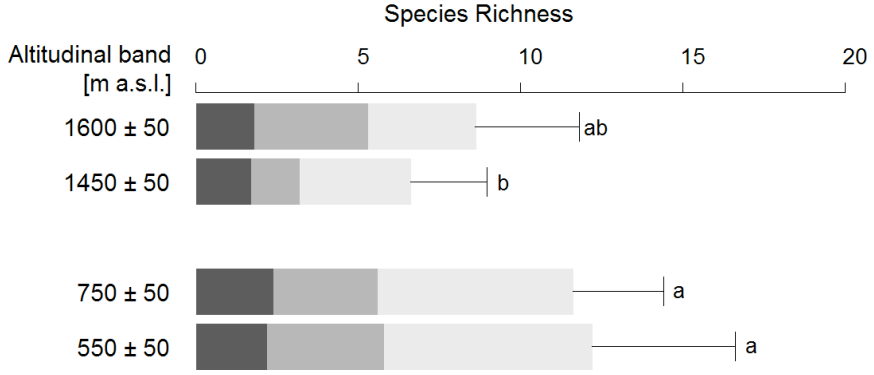

Figure 4. *Cumulative mean species richness for mosses (dark grey), herbaceous (grey), and woody plants (light grey) per altitudinal band. Error bars refer to total species richness showing its standard deviation. Lower case letters indicate significant differences in total species richness (Tukey HSD, $p < 0.05$).*

In all but one case, including the vegetation type as additional random factor, the model fit based on AIC values did not improve and none of them were significantly different from each other. The model AIC was smaller only in the case of woody plants if vegetation type was included as random factor as compared to the previous model. Moreover, the stepwise forward model selection confirmed all models with micro-relief heterogeneity, tree-density and northernness as fixed factors and altitudinal band as random factor as the best models based on AIC values, except for woody plants. For the latter, the best model included only tree-density and northernness as fixed factors but both altitudinal band and vegetation type as crossed random factors.

The investigation of the relative importance of small-scale heterogeneity within the different altitudinal bands by variance partitioning, showed strong differences both within and between the growth forms (Figure 6). Within each altitudinal band the proportion of variance explained by micro-relief heterogeneity was highest for mosses (up to 66% at 550 m.a.s.l.). However, there was no clear pattern observable with respect to altitude when the whole gradient was analysed. Nevertheless, the two different forest types (laurel and pine forest) showed a tendency towards decreasing influence of habitat heterogeneity with increasing elevation. While overall explained variance by micro-relief heterogeneity was highest in the lowest altitudinal band, it decreased at 750 m.a.s.l., increased again at 1450 m.a.s.l. and dropped to 20% towards the highest altitude. In contrast, micro-relief heterogeneity did not explain the variation in species richness patterns for herbaceous and woody plants, respectively.

Table 1. *Linear mixed-effects models of species richness (subdivided into mosses, herbaceous plants, woody plants and total species richness) and the corresponding environmental and spatial variables (micro-relief heterogeneity, tree density, northernness). The altitude was included as a random effect. Significant results ($p < 0.05$) are shown in bold. Df denotes the degrees of freedom.*

Explanatory variable	**Mosses**	**Herbaceous plants**	**Woody plants**	**Total species richness**
	p	***p***	***p***	***p***
Micro-relief heterogeneity	**0.0001**	0.0926	0.1901	**0.0008**
Tree density	0.0900	**<0.0001**	**0.0015**	**<0.0001**
Northernness	0.8997	**0.0019**	**0.0162**	**0.0055**
Df	33	33	33	33

4. Discussion

Our aim was to identify general tendencies in the effect of micro-relief heterogeneity on plant species richness. The results show a significant influence of micro-relief heterogeneity on overall plant species richness, which is in accordance with other studies [14,45,46]. Yet, broken down into growth forms, we found significant relationships across altitudinal bands only for mosses. This partly confirms our hypothesis, where we expected micro-relief heterogeneity to influence species richness of mosses and herbaceous plants more strongly than in the case of woody plants. However, the hypothesis that the influence of micro-relief heterogeneity increases with altitude had to be rejected for all growth forms (Figure 6). This might be due to the fact that relief heterogeneity *per se* only explained a small part of the variance in total species richness (namely 10%) and could therefore easily have been overlaid by other factors and processes such as tree density, anthropogenic disturbances, propagule pressure or patch size.

The chosen elevational gradient of more than 1000 m covers a strong gradient in tree species composition. Commonly two main forest types (laurel and pine forest) are differentiated. However, inclusion of the forest type did not improve the models. Disentangling an effect of forest type and elevation is a non-trivial task as forest structure and tree species composition change along elevational gradients. Micro-relief heterogeneity could explain more than 60% of the variance in moss species richness. However, herbaceous and woody plants did not show any response in the linear mixed effect models. On the one hand this could be due to the unequal response of vegetation layers to environmental gradients [47], or on the other hand to the fact that plant growth forms differ in their ability to respond to fine-scale variation in abiotic heterogeneity [48].

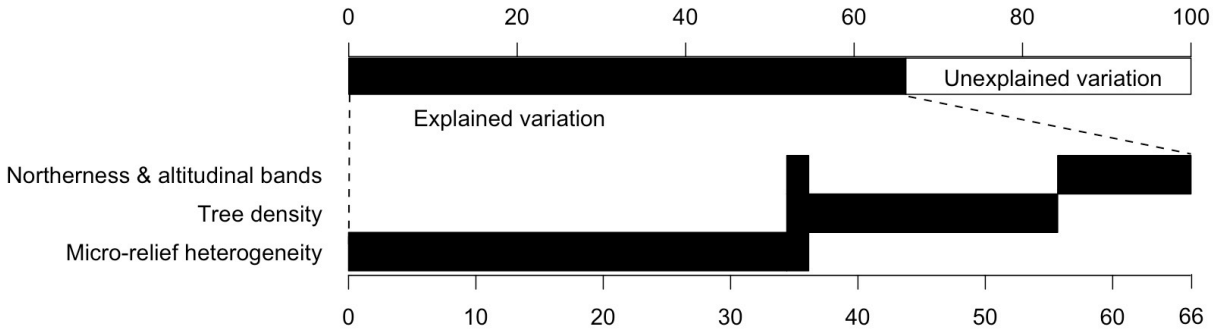

Figure 5. *Partitioning of the variation of total species richness between the explanatory variables tree density, a combined spatial variable based on northernness and altitudinal bands, and micro-relief heterogeneity. Overlapping bars indicate jointly explained variance [%]. Non-overlapping parts depict explained variance explained only by a single variable.*

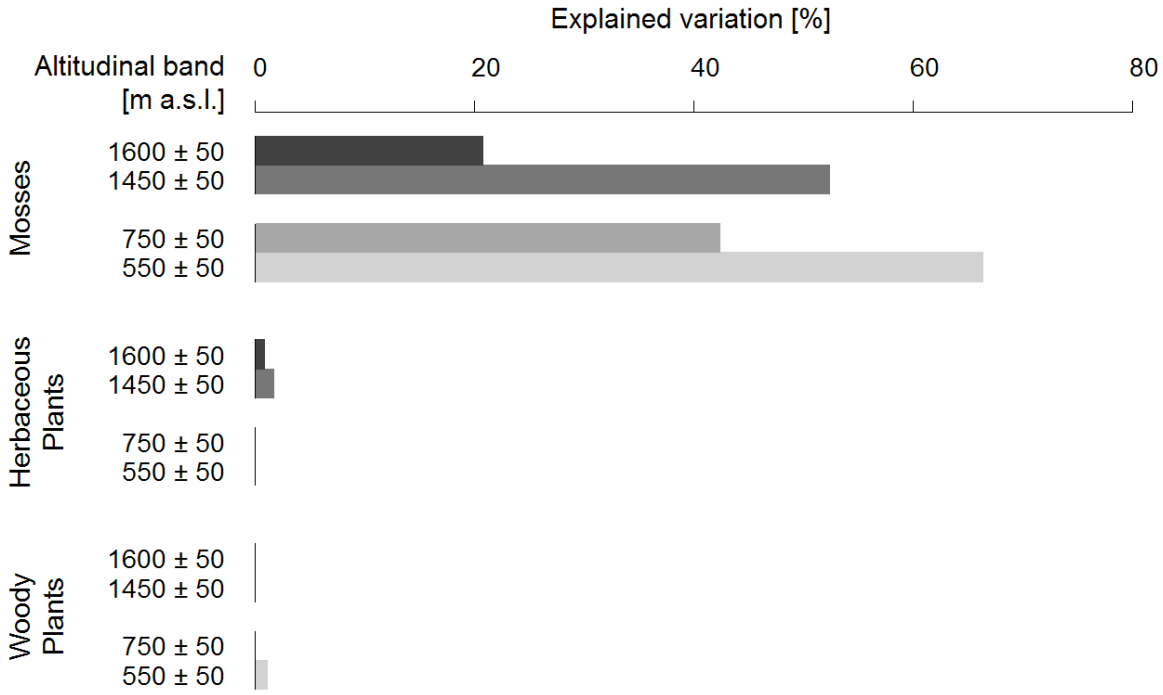

Figure 6. *Explained variation of species richness in percent (divided into mosses, herbaceous plants, woody plants and total species richness) by the explanatory variable micro-relief heterogeneity within the altitudinal bands.*

Total species richness increased significantly with increasing small-scale relief-heterogeneity (Table 1). Considering that only mosses responded significantly, the significant relationship of total species richness has to be interpreted as mainly driven by this group.

The influence of heterogeneous micro-relief conditions on mosses was expected and also apparent during field sampling. However, such scale dependent responses have not yet been systematically proven. Surface depressions presumably provide more moist conditions as compared to flat surfaces. Rocks and boulders provide additional types of substrate. Species not occurring on soils may occur on the stony surfaces thus boosting species numbers. Additionally, in pine forests often only plots comprising heterogeneous micro-relief were not covered by thick pine needle litter. However, it was astonishing that there was no effect of northernness or tree density detectable on moss species richness, as mosses profit from moist conditions [49], which are more likely to be found under denser canopies or on north facing slopes under this climate.

Tree density and northernness were found to serve as significant predictors for herbaceous and woody plants. In both cases species-poor plots were related to higher tree density, causing thick litter layers and shade, which might have prevented seedling establishment of other species. Northernness relates to aspect and in our case more precisely to the degree of potential irradiation: the lower the value for northernness, the higher the insolation, neglecting changes due to the diurnally changing influence of the trade-wind induced stratocumulus layer. In all cases the regression estimator for northernness was positive, which means that aspects with higher insolation host less species. This was especially unexpected for the herbaceous plants, as herbaceous richness generally profits from increased insolation in forests [50]. However, in the pine forests, where precipitation is a limiting factor for plant growth [51], the increased species richness on north-facing slopes might be explained by increased soil moisture found on north-facing plots.

In this study the scale of heterogeneity was chosen to be smaller than the spatial extent of individual woody plants, this scale may have been too fine for detection of relief effects on woody plants. As in a survey on the influence of spatial nutrient heterogeneity on species richness, Hutchings *et al.* [52] only found significant effects when the size of individual plants was

smaller than the measured scale. As the scale of observation (*i.e.*, 1 m) encompassed the actual size of the remaining growth forms and their presumed spatial range of influence, it can be assumed appropriate to detect the effect of relief heterogeneity on mosses and herbaceous plants. Whether the applied spatial resolution was sufficient, remains to be tested. Hofer *et al.* [10] labelled their 25 m^2 plots "microsites", which highlights the fact that even smaller resolutions are often not considered as being ecologically important. Our study emphasises that this assumption must be reconsidered. Heterogeneity is expected to act on different scales, especially when comparing growth forms as diverse as mosses and trees. Thus, we cannot conclude that heterogeneity *per se* does not affect plant richness of herbaceous or woody plants. This may depend on the grain and extent of studies [53]. For an investigation of such scale specific effects, studies with a nested plot design might be an appropriate approach.

A further factor masking the effect of micro-relief heterogeneity on herbaceous and woody species richness could have been the geographical isolation of the island, which limits the potential number of species able to colonize our plots (*sensu* [54]) and thus modifies the often found relationship between heterogeneity and diversity (e.g. [12]). Kadmon and Allouche [55] showed that the theory of island biogeography alters the relationship predicted by the niche theory.

We concentrated on forested ecosystems, where differences in micro-climate are expected to be small owing to limited insolation through dense canopies [56]. In open environments differences in micro-climate are likely to be more pronounced [5]. Nevertheless, the very fact that micro-climate does not mask other micro-relief induced factors such as the increase in surface availability per plot, the increase in substrate types or the small-scale variability in soil moisture, makes this analysis worthwhile. Moreover, as the growth form of mosses has shown, there is indeed an influence of micro-relief heterogeneity on species richness despite presumably moderate changes in microclimate.

5. Conclusions

In forest ecosystems of La Palma the species richness of various plant growth forms responds differently to surface structure. Only mosses respond directly to small-scale micro-relief heterogeneity, which increases the diversity of small-scale ecological niches independent of altitude. For small plants, such as mosses, bioclimatic envelope models might be based on too broad assumptions, even if local effects may by dampened on a larger scale [57]. However, for herbaceous and woody plants small-scale micro-relief heterogeneity does not contribute to an improved explanation of species richness patterns. For these species, general site conditions can be applied. Our results stress the fact that the role of relief heterogeneity has to be considered separately and specifically for different groups of organisms. There is no overarching relationship between relief heterogeneity and species richness across scales and plant growth forms. However, the influence of heterogeneity on herb, shrub and tree richness may vary with spatial resolution (grain size). Modern technology such as laser scanners may facilitate area-wide data collection and provide an opportunity to test this hypothesis. As species distribution models are a common predictive tool used for decision-making in nature conservation and for facing threats caused by climate change, an improved knowledge of the underlying ecological principles is crucial. Current modelling results might be strongly biased for species groups with small-scale habitats.

Acknowledgments

The study was supported by the "Global Change Ecology (M.Sc.)" study program within the Elite Network of Bavaria.

References

1. Parmesan, C.; Yohe, G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **2003**, *421*, 37–42.
2. Feeley, K.J.; Silman, M.R.; Bush, M.B.; Farfan, W.; Cabrera, K.G.; Malhi, Y.; Meir, P.; Revilla, N.S.; Quisiyupanqui, M.N.R.; Saatchi, S. Upslope migration of Andean trees. *J. Biogeogr.* **2011**, *38*, 783–791.

3. Thomas, C.D.; Cameron, A.; Green, R.E.; Bakkenes, M.; Beaumont, L.J.; Collingham, Y.C.; Erasmus, B.F.N.; de Siqueira, M.F.; Grainger, A.; Hannah, L.; *et al.* Extinction risk from climate change. *Nature* **2004**, *427*, 145–148.
4. Suggitt, A.J.; Gillingham, P.K.; Hill, J.K.; Huntley, B.; Kunin, W.E.; Roy, D.B.; Thomas, C.D. Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos* **2011**, *120*, 1–8.
5. Scherrer, D.; Körner, C. Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Glob. Change Biol.* **2010**, *16*, 2602–2613.
6. Alcamo, J.; Moreno, J.M.; Nováky, B.; Bindi, M.; Corobov, R.; Devoy, R.J.N.; Giannakopoulos, C.; Martin, E.; Olesen, J.E.; Shvidenko, A. *Climate Change 2007—Impacts, Adaptation and Vulnerability. Working Group II Contribution to the Fourth Assessment Report of the IPCC*; Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J., Hanson, C.E., Eds.; Cambridge University Press: Cambridge, UK, 2007; pp 541–580.
7. Scherrer, D.; Körner, C. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *J. Biogeogr.* **2011**, *38*, 406–416.
8. Hutchinson, G.E. Population studies—Animal ecology and demography—Concluding remarks. *Cold Spring Harb. Symp. Quant. Biol.* **1957**, *22*, 415–427.
9. Burnett, M.R.; August, P.V.; Brown, J.H.; Killingbeck, K.T. The influence of geomorphological heterogeneity on biodiversity I. A patch-scale perspective. *Conserv. Biol.* **1998**, *12*, 363–370.
10. Hofer, G.; Wagner, H.H.; Herzog, F.; Edwards, P.J. Effects of topographic variability on the scaling of plant species richness in gradient dominated landscapes. *Ecography* **2008**, *31*, 131–139.
11. Müller, C.; Berger, G.; Glemnitz, M. Quantifying geomorphological heterogeneity to assess species diversity of set-aside arable land. *Agric. Ecosyst. Environ.* **2004**, *104*, 587–594.
12. Lundholm, J.T. Plant species diversity and environmental heterogeneity: Spatial scale and competing hypotheses. *J. Veg. Sci.* **2009**, *20*, 377–391.
13. Loneragan, W.A.; Delmoral, R. The influence of microrelief on community structure of subalpine meadows. *Bull. Torrey Bot. Club* **1984**, *111*, 209–216.
14. Beatty, S.W. Influence of microtopography and canopy species on spatial patterns of forest understory plants. *Ecology* **1984**, *65*, 1406–1419.
15. da Silva, W.G.; Metzger, J.P.; Bernacci, L.C.; Catharino, E.L.M.; Durigan, G.; Simoes, S. Relief influence on tree species richness in secondary forest fragments of Atlantic Forest, SE, Brazil. *Acta Bot. Bras.* **2008**, *22*, 589–598.
16. Suchodoletz, H.V.; Glaser, B.; Thrippleton, T.; Broder, T.; Zang, U.; Eigenmann, R.; Kopp, B.; Reichert, M.; Zöller, L. The influence of Saharan dust deposits on La Palma soil properties (Canary Islands, Spain). *Catena* **2011**, in press.
17. Resler, L.M.; Butler, D.R.; Malanson, G.P. Topographic shelter and conifer establishment and mortality in an alpine environment, Glacier National Park, Montana. *Phys. Geogr.* **2005**, *26*, 112–125.
18. Debski, I.; Burslem, D.; Palmiotto, P.A.; Lafrankie, J.V.; Lee, H.S.; Manokaran, N. Habitat preferences of Aporosa in two Malaysian forests: Implications for abundance and coexistence. *Ecology* **2002**, *83*, 2005–2018.
19. Palmer, M.W.; White, P.S. Scale dependence and the species-area relationship. *Am. Nat.* **1994**, *144*, 717–740.
20. White, P.S.; Jentsch, A. The search for generality in studies of disturbance and ecosystem dynamics. In *Progress in Botany*; Esser, K., Lüttke, U., Kadereit, J.W., Beyschlag, W., Eds.; Springer: Berlin, Germany, 2001; volume 62, pp. 399–450.
21. Linhart, Y.B.; Grant, M.C. Evolutionary significance of local genetic differentiation in plants. *Annu. Rev. Ecol. Syst.* **1996**, *27*, 237–277.
22. Decocq, G. Patterns of plant species and community diversity at different organization levels in a forested riparian landscape. *J. Veg. Sci.* **2002**, *13*, 91–106.
23. Triantis, K.A.; Sfenthourakis, S. Island biogeography is not a single-variable discipline: The small island effect debate. *Div. Distrib.* **2011**, *18*, 92–96.
24. Whittaker, R.J.; Ladle, R.J.; Araujo, M.B.; Fernandez-Palacios, J.M.; Delgado, J.D.; Arevalo, J.R. The island immaturity—Speciation pulse model of island evolution: An alternative to the "diversity begets diversity" model. *Ecography* **2007**, *30*, 321–327.
25. Steinbauer, M.J.; Otto, R.; Naranjo-Cigala, A.; Beierkuhnlein, C.; Fernaández-Palacios, J.-M. Increase of island endemism with altitude—Speciation processes on oceanic islands. *Ecography* **2012**, *35*, 23–32.
26. Coblentz, D.D.; Riitters, K.H. Topographic controls on the regional-scale biodiversity of the south-western USA. *J. Biogeogr.* **2004**, 1125–1138.
27. Reyes-Betancort, J.A.; Guerra, A.S.; Guma, I.R.; Hurnphries, C.J.; Carine, M.A. Diversity, rarity and the evolution and conservation of the Canary Islands endemic flora. *An. Jard. Bot. Madr.* **2008**, *65*, 25–45.
28. Steinbauer, M.J.; Beierkuhnlein, C. Characteristic pattern of species diversity on the Canary Islands. *Erdkunde* **2010**, *64*, 57–71.
29. Fernandez-Palacios, J.M.; de Nicolas, J.P. Altitudinal pattern of vegetation variation on Tenerife. *J. Veg. Sci.* **1995**, *6*, 183–190.
30. Varela, A.M. Comparison of the aerosol index from satellites and the atmospheric extinction coefficient above the Canarian observatories. **2004**, *5489*, 245–255.
31. Irl, S.D.H.; Beierkuhnlein, C. Distribution of endemic plant species on an oceanic island—A geospatial analysis of La Palma (Canary Islands). *Procedia Environ. Sci.* **2011**, *7*, 170–175.

32. Arechavaleta, M.; Rodriguez, S.; Zurita, N.; Garcia, A. *Lista de Especies Silvestres de Canarias. Hongas, Plantas y Animales Terrestres*; Gobierno de Canarias.: Santa Cruz de Tenerife, Spain. 2010; p. 579.
33. Wilson, J.B. Cover plus: Ways of measuring plant canopies and the terms used for them. *J. Veg. Sci.* **2011**, *22*, 197–206.
34. Saleh, A. Soil roughness measurement—Chain method. *J. Soil Water Conserv.* **1993**, *48*, 527–529.
35. Dragut, L.; Eisank, C.; Strasser, T. Local variance for multi-scale analysis in geomorphometry. *Geomorphology* **2011**, *130*, 162–172.
36. Grohmann, C.H.; Smith, M.J.; Riccomini, C. Multiscale analysis of topographic surface roughness in the Midland Valley, Scotland. *IEEE Trans. Geosci. Remote Sens.* **2011**, *49*, 1200–1213.
37. Glenn, N.F.; Streutker, D.R.; Chadwick, D.J.; Thackray, G.D.; Dorsch, S.J. Analysis of LiDAR-derived topographic information for characterizing and differentiating landslide morphology and activity. *Geomorphology* **2006**, *73*, 131–148.
38. Haneberg, W.C.; Creighton, A.L.; Medley, E.W.; Jonas, D.A. Use of LiDAR to assess slope hazards at the Lihir gold mine, Papua New Guinea; CD-RPM. In *Proceedings of the International Conference on Landslide Risk Management*, Hungr, O., Fell, R., Couture, R., Eberhardt, E., Eds.; Vancouver, Canada, 31 May–3 June 2005.
39. Forman, R.T.T. *Land Mosaics: The Ecology of Landscapes and Regions*; Cambridge University Press: Cambridge, UK, 1995.
40. Pinheiro, J.; Bates, D.; DebRoy, S.; Sarkar, D. *nlme: Linear and nonlinear mixed effects models*; 3.1-100 version; 2011. Available online: http://cran.r-project.org/web/packages/nlme/index.html (accessed on 30 November 2011).
41. D. Bates; M. Maechler; Bolker, B. *lme4: Linear Mixed-Effects Models Using S4 Classe*; 0.999375–42 version; 2011. Available online: http://cran.r-project.org/web/packages/lme4/ index.html (accessed on 30 November 2011).
42. Oksanen, J.; Blanchet, F.; Kindt, G.; Legendre, R.; O'Hara, R.B.; Simpson, G.L. *Vegan: Community Ecology Package*; 1.17-10 version;, 2011. Available online: http://cran.r-project.org/web/packages/vegan/index.html (accessed on 30 November 2011).
43. Legendre, P. Studying beta diversity: Ecological variation partitioning by multiple regression and canonical analysis. *J. Plant Ecol. UK* **2008**, *1*, 3–8.
44. R Development Core Team; *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing: Vienna, Austria, 2011. Available online: http://www.R-project.org (accessed on 30 November 2011).
45. Johnson, M.P.; Frost, N.J.; Mosley, M.W.J.; Roberts, M.F.; Hawkins, S.J. The area-independent effects of habitat complexity on biodiversity vary between regions. *Ecol. Lett.* **2003**, *6*, 126–132.
46. Kuntz, K.L.; Larson, D.W. Microtopographic control of vascular plant, bryophyte and lichen communities on cliff faces. *Plant Ecol.* **2006**, *185*, 239–253.
47. Lyon, J.; Sagers, C.L. Structure of herbaceous plant assemblages in a forested riparian landscape. *Plant Ecol.* **1998**, *138*, 1–16.
48. Decocq, G. The 'masking effect' of silviculture on substrate-induced plant diversity in oak-hornbeam forests from Northern France. *Biodivers. Conserv.* **2000**, *9*, 1467–1491.
49. Almufti, M.M.; Sydes, C.L.; Furness, S.B.; Grime, J.P.; Band, S.R. Quantitative-analysis of shoot phenology and dominance in herbaceous vegetation. *J. Ecol.* **1977**, *65*, 759–791.
50. Anderson, K.L.; Leopold, D.J. The role of canopy gaps in maintaining vascular plant diversity at a forested wetland in New York State. *J. Torrey Bot. Soc.* **2002**, *129*, 238–250.
51. Nezadal, W.; Lindacher, R.; Welss, W. Local endemic plant species and phytodiversity of Western Canary Islands La Pama and La Gomera. *Feddes Repert.* **1999**, *110*, 19–30.
52. Hutchings, M.J.; John, E.A.; Wijesinghe, D.K. Toward understanding the consequences of soil heterogeneity for plant populations and communities. *Ecology* **2003**, *84*, 2322–2334.
53. Steinbauer, M.J.; Dolos, K.; Reineking, B.; Beierkuhnlein, C. Current measures for distance decay in similarity of species composition are influenced by study extent and grain size. *Glob. Ecol. Biogeogr.* **2012**, in press.
54. MacArthur, R.H.; Wilson, E.O. *The Theory of Island Biogeography. Monographs in Population Biology*; Princeton University Press: Princeton, NJ, USA, 1967.
55. Kadmon, R.; Allouche, O. Integrating the effects of area, isolation, and habitat heterogeneity on species diversity: A unification of island biogeography and niche theory. *Am. Nat.* **2007**, *170*, 443–454.
56. Paulsen, J.; Korner, C. GIS-analysis of tree-line elevation in the Swiss Alps suggests no exposure effect. *J. Veg. Sci.* **2001**, *12*, 817–824.
57. Leuzinger, S.; Luo, Y.Q.; Beier, C.; Dieleman, W.; Vicca, S.; Korner, C. Do global change experiments overestimate impacts on terrestrial ecosystems? *Trends Ecol. Evol.* **2011**, *26*, 236–241.

9. Manuscript 8 - An eleven-year exclosure experiment in a high-elevation island ecosystem: Introduced herbivore impact on shrub species richness, seedling recruitment and population dynamics

Journal of Vegetation Science 23 (2012) DOI: 10.1111/j.1654-1103.2012.01425.x

Authors: Severin David Howard Irl[1,2,*], Manuel Jonas Steinbauer[2], Wolfgang Babel[3], Carl Beierkuhnlein[2], Gesche Blume-Werry[2], Jana Messinger[2], Ángel Palomares Martínez[4], Stefan Strohmeier[5], Anke Jentsch[1]

[1] *Dept. of Disturbance Ecology, University of Bayreuth, D-95447 Bayreuth, Germany*
[2] *Dept. of Biogeography, University of Bayreuth, D-95447 Bayreuth, Germany*
[3] *Dept. of Micrometeorology, University of Bayreuth, D-95447 Bayreuth, Germany*
[4] *National Park Caldera de Taburiente, La Palma, E-38750 El Paso, La Palma, Spain*
[5] *Dept. of Soil Ecology, University of Bayreuth, D-95447 Bayreuth, Germany*
*Correspondence: Severin D. H. Irl, Phone: +49-921-552307, Fax: +49-921-552315,
E-mail address: severin.irl@uni-bayreuth.de

Abstract
Questions Do introduced herbivores and fire explain the mono-dominance of one legume shrub (*Adenocarpus viscosus* ssp. *spartioides*) above the tree line on an oceanic island given the fact that a number of other legume shrub species are potentially present? What drives the observed landscape scale life-death pattern within the mono-dominant shrub species population?
Location The subalpine scrub vegetation of La Palma (Canary Islands, Atlantic Ocean).
Methods An eleven-year exclosure experiment with sites distributed along an elevation and orientation gradient was used to identify the influence of introduced herbivore pressure on four endemic shrub species and their seedling recruitment. Further, we assessed the population dynamics and spatial pattern of the dominant shrub species *A. viscosus* ssp. *spartioides*. Habitat and vitality characteristics were investigated assessing spatial topographic features and tree ring based age estimates. Linear mixed models, ANOVA's, linear regression and variation partitioning were used as statistical analysis tools.
Results Outside of the exclosures *A. viscosus* ssp. *spartioides* was virtually mono-dominant in the study area, even though other shrub species seem better suited in the absence of introduced herbivores. The presence of introduced herbivores significantly reduced seedling recruitment within all target species, except for *A. viscosus* ssp. *spartioides*. Mean age of *A. viscosus* ssp. *spartioides* increased with elevation, although vitality analyses indicated that the subalpine scrub is elevated above its growth optimum. Three out of four investigated shrub species showed differences in growth height depending on elevation and island orientation.
Conclusion Introduced herbivores and fire are identified as key disturbances enhancing the occurrence of *A. viscosus* ssp. *spartioides,* a commonly less competitive species. However, *Genista benehoavensis*, a single island endemic shrub species, seems to be better adapted to the harsh climatic conditions of the subalpine scrub in the absence of introduced herbivores than any other shrub species.

Keywords: alien herbivore; competition; fenced plots; invasive mammals; legume shrub; European rabbit; summit scrub; Canary Islands; shrub community, oceanic island

Abbreviations: ANOVA = analysis of variance; V_i = vitality index

Nomenclature: Acebes Ginovés et al. (2010)

Introduction

Island ecosystems rich in endemic species have often evolved under reduced ecological pressures, for example, where the influence of herbivory or competition is low (Bowen & van Vuren, 1997; Nogales et al., 2006). Especially the combination of habitat degradation or change through human disturbances and the introduction of non-island species have lead to massive problems in isolated island ecosystems (Vitousek et al., 1997; Campbell & Donlan, 2005, Caujapé-Castells et al., 2010). Introduced species generally arrive on islands without their natural array of pests and diseases, which often gives them a competitive advantage over native species (Darwin, 1859; Simberloff, 1995; Courchamp et al., 2003). In particular, introduced herbivores such as feral goats (*Capra hircus*) or rabbits (*Oryctolagus cuniculus*), both among the world's 100 worst invasive species (Lowe et al., 2000), have had detrimental effects on native island biota, degrading complete ecosystems to a state where regeneration without herbivore eradication is (nearly) impossible (e.g. Galapagos (Campbell & Donlan, 2005), Canary Islands (Garzón-Marchado et al., 2010), Hawaii (Mueller-Dombois & Spatz, 1975), Santa Catalina Island (Coblentz, 1978), and New Zealand (Parkes, 1990)).

Introduced herbivores have established themselves, among other ecosystems, in the high-elevation ecosystem of the oceanic island La Palma, Canary Islands (Palomares Martínez et al., 2004; Garzón-Marchado et al., 2010). There, the subalpine scrub has a long legacy of goat grazing. In recent decades rabbits have become the number one herbivore due to the abolition of goat grazing for economic and conservational reasons (Garzón-Marchado et al., 2010). Nevertheless, the vegetation dynamics we witness today are probably still being influenced by the legacy of goat grazing in historic times (see Kyncl et al. (2006) for the subalpine scrub of Tenerife). Additionally, the high-elevation ecosystem of La Palma is an interesting study objects because of its comparatively low species richness, yet high degree of endemism (Steinbauer et al., 2011; Irl & Beierkuhnlein, 2011).

In the transitional zone between tree line and alpine environments, shrubs are the dominant growth form on many oceanic islands including the Canary Islands (Lausi & Nimis, 1986; Kyncl et al., 2006,), the Cape Verde Islands (Leuschner, 1996), La Réunion (Strasberg et al., 2005), Crete (Kazakis et al., 2007) and Hawaii (Leuschner, 1996). Often, subalpine ecosystems are dominated by very few to only one key shrub species.

Shrubs in general have been found to act as ecosystem engineers influencing multiple levels of biological organization (e.g. Cushman et al., 2010). N-fixing legume shrubs are considered to be key pioneer species often dominating primary successional stages (Walker et al., 2003; González et al., 2010) and invading non-native habitats (Shaben & Myers, 2010), but also reaching competitive dominance (MacArthur & Levins, 1967; Callaway & Ridenour, 2004; Hierro et al., 2005).

Although situated off the NW-African coast, the high-elevation scrub of the Canary Islands floristically resembles communities found in comparable elevations of the Mediterranean islands (Brullo et al., 2008). On La Palma *Adenocarpus viscosus* ssp. *spartioides*, a single island endemic legume shrub on the subspecies level, forms an almost mono-dominant cover in the subalpine scrub – sometimes also called the summit broom scrub (Garzón-Machado et al., (2011) –, even though other functionally similar endemic, but highly endangered shrub species are present (del Arco Aguilar et al., 2010). Above the *Pinus canariensis*-forests (called *pinar*) one can observe a distinct pattern in the *A. viscosus* ssp. *spartioides* subalpine scrub (hereafter *codesar*). A high vegetation cover, yet seemingly random distribution of living, half-dead and dead individuals is a common sight on the densely populated outer flanks of the caldera (Fig. 1), while the almost vertical rocky inner flanks cannot support any type of closed vegetation cover.

We use the example of the *codesar* on La Palma to assess the ecological effect of introduced herbivores on shrub species and their interaction with other key disturbances (i.e. fire, ice storms) and try to gain insights into the mechanisms that control the landscape-scale life-death pattern of *A. viscosus* ssp. *spartioides*. We ask the following research questions: (a) Which factors explain the mono-dominance of one legume shrub above the tree line on an oceanic island

best, given the fact that a number of other legume shrub species are potentially present? (b) Which factors drive the observed landscape-scale life-death pattern of living and dead components within the *A. viscosus* ssp. *spartioides* population?

Methods

Study area

The study took place in the high altitudinal zone of La Palma. The Canary Islands are located near the African coastline between 27° and 29° northern latitude and 14° and 18° western longitude. The archipelago is of volcanic origin and consists of seven main islands larger than 250 km^2. Covering 708 km^2 La Palma is the third smallest island (Carracedo et al., 2002) and being around 1.7 Ma old, it is among the youngest islands of the archipelago (maximum age: 20.5 Ma for Fuerteventura; Fernández-Palacios & Whittaker, 2008) expressing steep environmental gradients (Irl & Beierkuhnlein, 2011). The study area is situated on the outer flanks of the rim of the Caldera de Taburiente on the Northern part of La Palma (Fig. 2), ranging from about 1800 m a.s.l. to the top of the rim at around 2400 m a.s.l., and covers 14.3 km^2. The field survey focusing on the population structure of *Adenocarpus* as well as browsing was conducted in February 2008. Data from the exclosure experiment regarding inter-specific competition and recruitment were collected in April 2011.

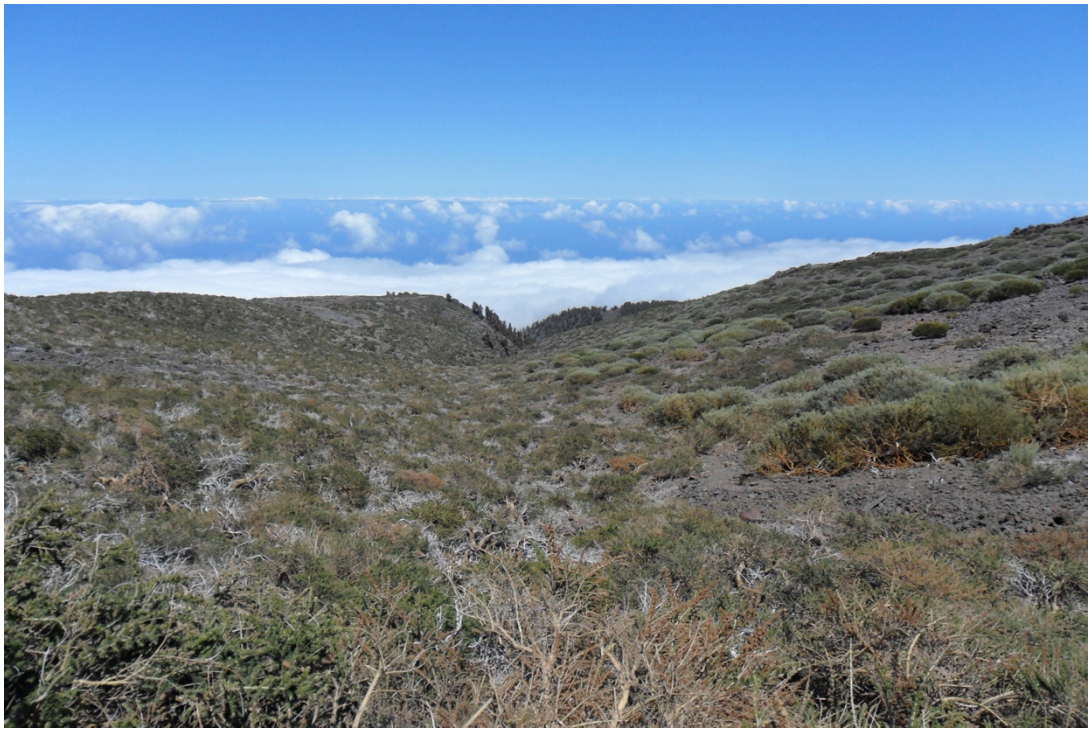

Figure 1. Seemingly random pattern of living, half-dead and dead individuals of *Adenocarpus viscosus* ssp. *spartioides* on the densely populated outer NE-flanks of the Caldera de Taburiente at around 2150 m a.s.l. (at Defront and left). The right side shows a NP exclosure site, where the fence has been removed to enable natural regeneration. Here, shrub species diversity is higher, especially well visible are *Genista benehoavensis* (greyish-green) and *Spartocytisus supranubius* (dark-green). Unfortunately, *Adenocarpus* was removed during the deconstruction of the fence, thus this picture does not resemble a true natural stand. The *Genista* individuals in the foreground on the right-hand side already show browsing marks. The *Pinus canariensis*-treeline in the background approaches approximately 2000 m a.s.l.. In addition, the clouds of the thermal inversion layer can be seen in the background. (Photo: M.J. Steinbauer, April 2011).

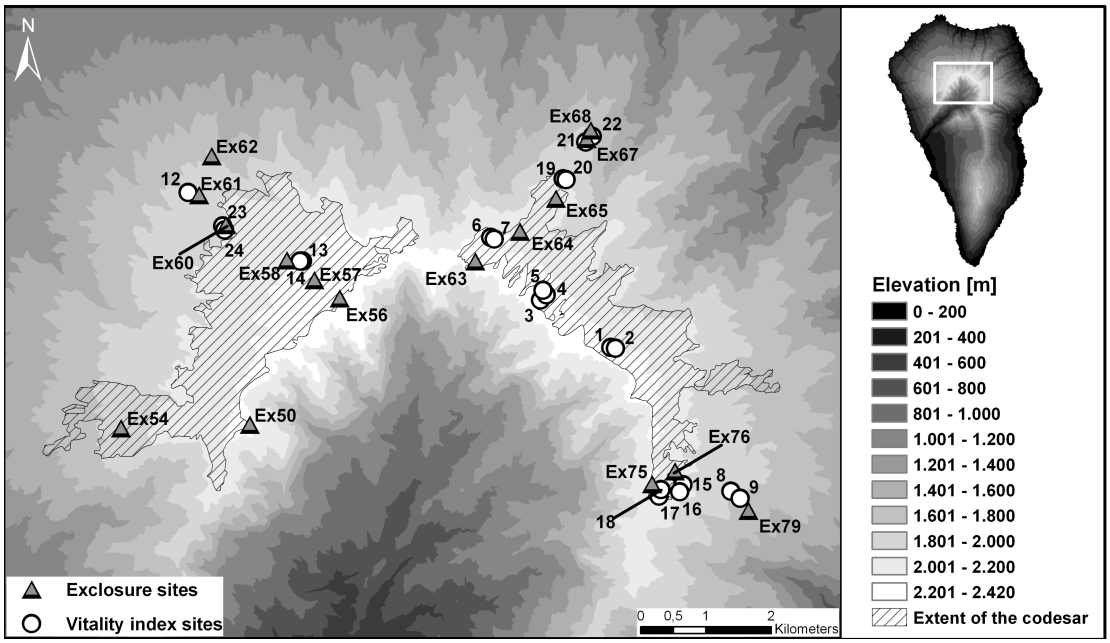

Figure 2. Site location on the Caldera de Taburiente. Circles illustrate the V_i sites, squares the plots for the age/circumference-correlation and triangles the fenced exclosure sites, where growth height was measured. The shaded area depicts the current extent of the *codesar* (Digital elevation model provided by Dr. Félix Medina of the *Consejería de Medio Ambiente del Cabildo Insular de La Palma*; map created in ArcView 9.3.1).

The thermal inversion (above 1200 m in summer and 1700 m in winter) created by humid trade winds blowing from the NE against the mountainside effectively impedes the convective and orographic rise of moist air masses towards the summits. Therefore, factors like high solar radiation, extensive arid periods of up to 6 months, high temperature amplitudes and harsh irregular winter conditions in the form of ice and snow influence plant growth strongly (González Henríquez et al., 1986). Furthermore, variation in annual precipitation is very high in the subalpine zone, e.g. ranging from 350 to 2480 mm within one station (Morro de la Cebolla, 2150 m). The mean annual temperature (9.3ºC) and precipitation (369 mm/a) of Izaña (2367 m) on the neighbouring island of Tenerife could be attributed to the subalpine scrub of La Palma (González Henríquez et al., 1986), although the measurements conducted by the National Park (NP) Caldera de Taburiente suggest that La Palma receives more precipitation at comparable altitudes. Similar to the subalpine scrub of Tenerife, the legume shrub dominated *codesar* is found on well-developed andosols (Brullo et al., 2008) on the gentle slopes of the outer flanks.
As archaeological findings suggest, the feral goat (*C. hircus*) was introduced more than 2000 years ago by the aboriginal inhabitants (Navarro et al., 1990), while the European rabbit (*O. cuniculus*) was brought to La Palma in the 15th and 16th century by the Castilian conquerors and is now partially controlled by hunting (Cabrera-Rodríguez, 2006). Several other introduced species can be found, such as rats (*Rattus* spp.), also introduced by the conquerors, or the Saharan *arruí* goat (*Ammotragus lervia*; Nogales et al., 2006), deliberately introduced by the National Institute for Environmental Conservation (ICONA) to the National Park in the 1970s to stimulate big game hunting as a new economic field. In general, no native mammalian key herbivore naturally exists or has ever existed in the subalpine scrub of La Palma or on any other island of the Canary archipelago (Traveset et al., 2009).
Fire is another important natural disturbance shaping this ecosystem. In addition to this goat herdsmen regularly burned the *codesar* once it reached an impassable size and density for herding. Nonetheless, fire frequency (probably less than every 10 years) and intensity has increased in the last decades due to an increase in human-induced fires (Höllermann, 2000; Palomares Martínez et al., 2004). One reason for this is an accumulation of fuel that has been

registered due to the ceasing of wood and pine needle extraction. Although fire management is taken seriously by local fire departments, wildfires often spread from the fire-adapted *pinar* up into the treeless subalpine scrub at irregular intervals and intensities.

Study species

The island endemic *Adenocarpus viscosus* ssp. *spartioides* Rivas-Mart. & Belmonte is a member of the Fabaceaen family (González Henríquez et al., 1986). It produces bright yellow flowers, has small evergreen leaves and a strongly ramified, but rather compact growth form (González Henríquez et al., 1986). The upper surface of its leaves is covered with small spiral hairs, while the bottom side is densely coated with subsessile glands, both morphological traits typical for semi-arid high-elevation vegetation (Lausi & Nimis, 1986). Year rings are produced in its woody branches that reflect a pronounced seasonality in growing conditions.

A. viscosus ssp. *spartioides* is attributed to the Genisto benehoavensis-Adenocarpetum spartioides Santos 1983 nom. mut. (art. 45) Rivas-Martínez et al. 2001, a subalpine dry open scrub community with ecological similarities to the Spartocytisetum supranubii Oberdorfer ex Esteve 1973 nom. mut. (art. 45) Rivas-Martínez et al 2001 of Tenerife both being part of the alliance Spartocytision supranubii (Leuschner, 1996). Fabaceaean species play an important role in all of these communities on comparably young soils in a harsh climate, probably due to their advantageous trait of being able to fix nitrogen.

Today, *A. viscosus* ssp. *spartioides* exhibits virtually mono-dominant stands in the subalpine zone of La Palma. However, a transition zone with the *pinar* exists below the timberline, where our target species contributes substantially to the performance of the vegetation. Its altitudinal amplitude reaches from 1500 to 2400 m a.s.l., although its zone of optimal growth occurs between 1700 and 2000 m a.s.l. (González Henríquez et al., 1986). However, it is not clear, whether the subalpine zone is climatically induced or if it is anthropogenically influenced (see e.g. Leuschner, 1996).

Shrub species diversity of the entire subalpine community has become strongly pauperized through goat and rabbit grazing (Cabrera-Rodriguez, 2008), increased fire frequencies and human disturbances such as collecting branches for firewood and fodder (Palomares Martínez et al., 2004). For this reason, the National Park management of the NP Caldera de Taburiente heads a conservation initiative for endangered native and endemic species. Endangered species include shrubs such as *Bencomia exstipulata*, *Chamaecytisus proliferus* ssp. *proliferus*, *Genista benehoavensis*, *Spartocytisus supranubius* and *Teline stenopetala* ssp. *sericea* (hereafter only genus names will be used; Palomares Martínez et al., 2004). *Genista* is a single island endemic to La Palma, while *Bencomia* and *Spartocytisus* are also found in the subalpine scrub vegetation of Tenerife (Acebes Ginovés et al., 2010). *Adenocarpus* and *Teline* are single island endemic subspecies (Acebes Ginovés et al., 2010). *Chamaecytisus* is found on several other islands of the archipelago. A variety of this species that is endemic only to La Palma is described but not generally accepted (var. *calderae*; Nezadal et al., 1999). Many of these characteristic species have become extremely rare or have nearly been driven to extinction. However, they are still found on inaccessible cliffs and rocky outcrops. In recent years, these historically important species have been sown in their natural habitats in protected exclosures established by the National Park authorities (Palomares Martínez et al., 2004).

Sampling design: factors driving mono-dominance

In this study, seven rectangular 20 x 20 m exclosure plots established by the National Park in 2000 were used to assess the growth potential and competitive success of the present shrub species (*Adenocarpus*, *Bencomia*, *Chamaecytisus*, *Genista, Spartocytisus* and *Teline*) in the absence of herbivores (Fig. 2 and Tab. 1). All vegetation was removed within the exclosures in 2000 and an equal amount of seeds per species (*Genista* and *Spartocytisus*: 3000 seeds/plot; *Teline* and *Chamaecytisus*: 2000 seeds/plot; *Bencomia*: 30000 seeds/plot) was sown (note that seed numbers per species varied strongly due to highly differing germination success between species, as experimentally tested by Palomares Martínez (1993)). We assumed that seeds of

Adenocarpus were also present in the seed bank, as this species is omnipresent in the study area. In addition, seeds of the sown shrub species were presumed to be present inside and outside the exclosures in equal quantities because species reach regeneration age after 2 to 5 years (Palomares Martínez, 1993) and natural seed dispersal has therefore been possible for about 6 to 9 years. The plots are fenced and regularly monitored. They differ in altitude and orientation. Only those plots where the access of herbivores was efficiently impeded and no signs (faeces, browsing marks) of their influence were found, were used for biometric measurements. *Bencomia* and *Teline* were excluded from analysis, due to the low number of individuals found in the exclosures. For all other shrub species, growth height of each individual was measured. A control plot of similar size was placed next to the exclosure and growth height of twenty randomly selected individuals of each shrub species was measured here as well.
To study the effect of herbivore presence on rege-neration of established plant species, 10 subplots of 1 m^2 were randomly selected in eleven exclosures and the associated outer plots. Present seedlings (i.e. not yet lignified individuals) of either shrub species were counted. We selected all exclosures that were neither disturbed (e.g. by fire) nor entered by herbivores within the last two years (Fig. 2 and Tab. 1). This resulted in a larger number of suitable sites than those used for the biometric measurements where the criterion was eleven years without disturbance. Note that due to time constraints, some plots included in the biometric measurements were not assessed for the seedling establishment.

Sampling design: life-death pattern of Adenocarpus
In a second step, plotless and transect sampling methods were applied, due to the high density and the partial impassibility of the *codesar*, to assess the pattern of living versus dead organs of *Adenocarpus*. Altitudinal and aspect transects were placed along the caldera flanks. 22 sites (sites 1-9 and 12-24, Fig. 2) were sampled roughly located at three altitudinal levels (transition zone of the *codesar* and the *pinar* between 1800 and 2000 m, mid-*codesar* between 2000 and 2200 m and high-*codesar* above 2200 m) and at three different caldera (macro-) orientations (E, NE, NW; note: the northern flank of the caldera is extremely steep and rocks are too instable for access) with additional plots at the caldera rim. Two sites with different slope (micro-) aspects were selected at each altitudinal level and aspect. 16 randomly selected *Adenocarpus* individuals were sampled for each site. Furthermore, measurements for each site included slope aspect and angle, elevation, maximum growth height per species, circumference of the thickest branch per species and the vitality index V_i. The vitality index V_i describes the estimated percentage of green leaf coverage relative to the number of branches (i.e. V_i: 0 = 0% percentage of green leaf coverage relative to the number of branches, dead; 1 = 1 - 24%; 2 = 25 - 74%; 3 = 75 - 99%; 4 = 100%). For example, a shrub individual with a $V_i = 3$ had about three-quarters of its branches covered with green leaves.

Table 1. Overview of the exclosure sites used for growth height and seedling recruitment measurements. For the exact location please compare with map in Fig. 2.

Site	Growth height	Seedling recruitment
Ex50	x	
Ex54	x	
Ex56	x	
Ex57		x
Ex58	x	x
Ex60		x
Ex61		x
Ex62		x
Ex63	x	
Ex64		x
Ex67		x
Ex68		x
Ex75	x	
Ex76	x	x
Ex79		x

Besides direct ecological impacts, the performance of the subalpine scrub ecosystem depends also on age structure and population diversity. Therefore, 50 randomly selected branches of *Adenocarpus* individuals were cut to count growth rings. *Adenocarpus* branches generally ramify directly from the point, where the stem protrudes from the soil. A preliminary investigation

showed that the thickest branch gives a good estimation of plant age and was therefore used for counting growth rings. In 12 cases of undifferentiated tree rings individuals were excluded from the analysis. A multiple regression with age as dependent variable and circumference and growth height as explanatory variables (including interaction; r^2 of 0.79***, Fig. S1 in supporting information) showed the best age estimate and was therefore preferred to a simple circumference/age correlation (r^2 of 0.57*** Fig. S1 in supporting information). In further analyses the variable "age" is always derived via the interacting relation.

Statistical Analysis

Significant differences in mean growth height between the shrub species within each exclosure were assessed using ANOVA with a post-hoc Tukey test. In addition, all exclosure sites were combined to one analysis using linear mixed models (R-package "nlme" version 3.1-96; Pinheiro et al. 2009) with site as random variable. Again significance was tested using ANOVA with a post-hoc Tukey test. The latter one is implemented in R package "multcomp" (Hothorn et al. 2008). A high number of young and thus small individuals could bias the comparison of mean maximum growth height. Therefore, we additionally restricted our analysis to large individuals (> 2/3 of the growth height of the largest individual of a certain species on a certain site). Finally, linear regression (with r^2 as goodness-of-fit indicator) was applied to quantify the effect of altitude and caldera orientation of the exclosure sites on growth height. The effect of caldera orientation was tested on the residuals of the linear regression on altitude.

To gain an understanding on the effect of herbivory on seedling establishment, linear mixed models were implemented for each investigated shrub species. We checked whether the number of established seedlings was significantly higher inside or outside of herbivore exclosures. "Site" was selected as random variable to account for possible differences among the plots.

In order to differentiate the joined and independent explanatory power of the essential driving factors, all variables significantly ($p>0.001$) correlating with V_i (elevation, age, slope aspect and caldera orientation), were compared by a variation partitioning using multiple linear regression models (linear regression and adjusted r^2 as the goodness-of-fit measure) following the guidelines of Legendre (2008).

All analyses and graphics were performed in R (R Development Core Team, 2010). Significance is indicated by * for $p<0.05$, ** for $p<0.01$ and *** for $p<0.001$.

Results

Factors driving mono-dominance

In the absence of herbivory, *Genista* and *Chamaecytisus* are able to grow higher than *Adenocarpus* and *Spartocytisus*. This is true if all individuals (Fig. 3) or if only the large ones (Fig. S2 in supporting information) are compared. However, *Adenocarpus* shows the highest number of individuals in all sampled exclosure sites. No other adult shrub species besides *Adenocarpus* was found outside the fenced sites, where herbivores have unlimited access. If parts of individuals of non-*Adenocarpus* species reached beyond the fence, they were heavily browsed (Fig. 4).

Growth height decreases with elevation at a rate of 8.40 cm/100 m*** (9.4%/100 m; percentage values are calculated in relation to mean growth height) for *Adenocarpus*, 10.6 cm/100 m* (5.9%/100 m) for *Genista* and 17.9 cm/100 m*** (17.5%/100 m) for *Spartocytisus,* while no relation was detected for *Chamaecytisus*.

After correcting for the effect of elevation, a lower growth height of *Adenocarpus* was detected for NW (-52.4 cm***) and W (-22.0 cm) facing sites. *Chamaecytisus* also grows smaller on NW (-94.4 cm*) and W (-52.1 cm*) facing sites, while *Spartocytisus* has a lower growth height on NW sites (-67.8***). No tendency was detected for *Genista,* which seems to be less affected by caldera orientation.

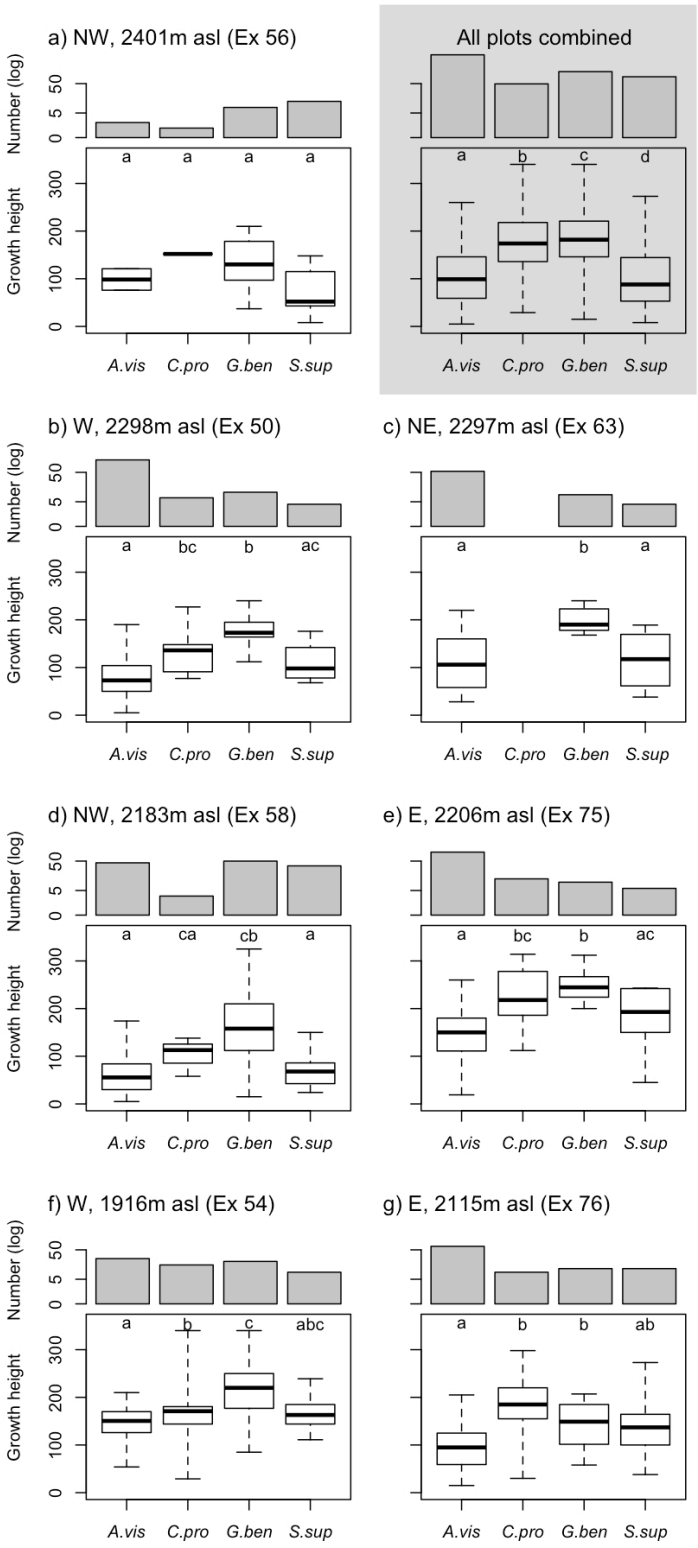

Figure 3. Growth heights of different shrub species according to altitude and island orientation measured in exclosure plots established in 2000 (maximum individual age of 11 years). Box-plots indicate growth height with whiskers extending to the data extremes. The grey barplots depict the number of measured individuals. Lower case letters indicate significant differences ($p<0.05$). Graphs (a-g) are sorted from top to bottom according to elevation and from left to right according to island orientation. The graph shaded in grey shows the complete dataset. Abbreviations: *A.vis = Adenocarpus viscosus* spp. *spartioides, C.pro = Chamaecytisus proliferus* ssp. *proliferus, G.ben = Genista benehoavensis, S.sup = Spartocytisus supranubius*.

The mean number of seedlings per subplot (1 m^2) without herbivore pressure was 1.30 ±5.91 for *Adenocarpus,* 0.22 ±0.78 for *Chamaecytisus*, 0.05 ±0.21 for *Spartocytisus* and 0.07 ±0.26 for *Genista*. Outside the fences the mean number of seedlings dropped to 0.33 ±1.04 per patch for *Adenocarpus,* while overall only one *Chamaecytisus* seedling and none of the other species was found (Fig. 5). Given the high standard deviation the mixed effect models result in a significant higher seedling number for *Chamaecytisus***, *Spartocytisus** and *Genista*** inside the fences, but no significant difference for *Adenocarpus* (p = 0.068).

Figure 4. Photo of white-blooming *Chamaecytisus proliferus* ssp. *proliferus* reaching from inside an exclosure plot (right-hand side) out into the potential reach of introduced herbivores. Browsing marks are visible on the left-hand side of the fence indicating the maximum height to where herbivores may reach. The picture was taken on the E side of the caldera at around 1800 m a.s.l. (i.e. the transition zone of the Canary Pine forest to the subalpine scrub). (Photo: M.J. Steinbauer, April 2011).

Life-death pattern of Adenocarpus

The vitality index V_i exhibits a spatial pattern: vitality is negatively correlated to age (Fig. 6a) and tends to be lower in higher elevations and on the northeastern side of the caldera rim. The age of an individual is the main influence concerning the vitality of *Adenocarpus* explaining 33.5% of variation (in the linear model for variation partitioning). The older plots exhibit lower vitality than the younger plots. Moreover, the variance of the V_i data is higher on the older plots; hence the younger plots are apparently more homogeneous in vitality (see also Fig. S3 in supporting information). Elevation explains 15.2% of the variance of the V_i in the dataset. 10.6% and 6.6% of the variance are explained by slope aspect and caldera orientation, respectively. Variation partitioning reveals that age provided the largest share of explained variation either independently (46%) or jointly with elevation (20%). Only a minor part of the explained variation (4%) is contributed independently from age and elevation (Fig. 7).

Age of *Adenocarpus* individuals is positively related to elevation (Fig. 6b), i.e. higher located sites host populations with a significantly higher mean age than the sites at mid-elevations and in the *pinar*. Sites with a relatively high mean age show a distinct higher variance than young growth sites (Fig. S3 in supporting information).

Discussion

Mono-dominance of Adenocarpus

Adenocarpus is virtually mono-dominant in the subalpine scrub vegetation of La Palma. In the plots next to the exclosures no adult shrub species other than *Adenocarpus* are present, even though seed dispersal from other shrub species such as *Bencomia*, *Chamaecytisus*, *Genista*, *Spartocytisus* and *Teline* from inside the exclosure can be expected due to advanced age, large size and abundant flowers of many target shrubs. However, some adult individuals of the non-*Adenocarpus* shrub species are locally found outside of the exclosures throughout the subalpine scrub independently of the studied exclosures. Damage and consumption by introduced herbivores, which has been suggested to be one of the four major threats to Canarian endemic plant diversity (Francisco-Ortega et al., 2000), to *Adenocarpus* is by far lower than to any of its other competitor species. This selective grazing, a common phenomenon among herbivores (van Vuren & Coblentz, 1987; Bryant et al., 1991; Rafferty & Lamont, 2007; Traveset et al., 2009; Maher et al., 2010), gives *Adenocarpus* an advantage over other shrub species. Hence, herbivores potentially eliminate non-*Adenocarpus* species from the vegetation cover and restrict them to areas that are outside of their reach, such as rocky outcrops and cliffs (Garzón-Machado et al., 2011). Personal observations in plots, where rabbits managed to enter, support the idea of a selective grazing as only 10% of *Adenocarpus* individuals showed browsing marks, while all other shrubs were heavily damaged (90-100% browsing marks).

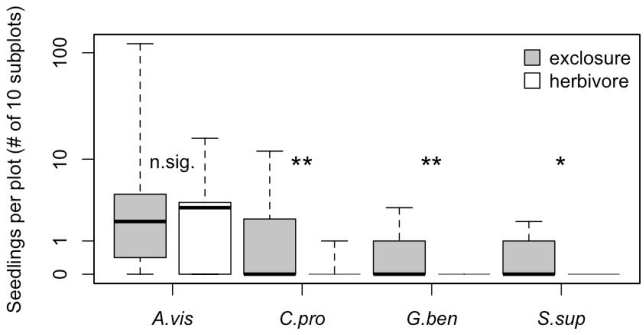

Figure 5. Seedling recruitment of the four target shrub species inside and outside of the exclosures. Seedling recruitment of all species, except for *Adenocarpus*, decreases significantly from inside to outside of the exclosure displaying the strong negative effect of introduced herbivore presence. Significance is based on mixed effect models of the subplot data. Abbreviations as in figure 3. Whiskers extend to the data extremes.

Phytochemical analyses have shown that *Adenocarpus* possesses a variety of different alkaloids that could potentially act as defence mecha-nisms towards mammalian herbivory. Among other alkaloids such as toxic pyrrolizidines (Cheeke, 1988; Grein-wald et al., 1992), the main alkaloid, adenocarpine, probably leads to a reduced palatability and digestibility in herbivores. It is a structural deri-vative of the toxic anabasine found in *Nicotiana glauca* (Schütte et al., 1964) and is particularly enriched in the leaves (Greinwald et al., 1992). The only other species possessing significant amounts of alkaloids (i.e. mainly sparteine) was *Chamaecy-tisus*, but the amounts showed a pronounced seasonality with high values in spring and low values in fall (Ventura et al., 2000). High values of sparteine significantly reduced sheep performance and the consumption of *Chamaecytisus* in spring, if herbivores were given the choice (Ventura et al., 2000).

Seedling recruitment in all species is very low. However, *Adenocarpus* is strongly favoured in this respect. It seems to react more or less indifferently to herbivore pressure, even though a tendency towards higher recruitment within the exclosures is discernable. Seedling recruitment of the other species is minimal (*Chamaecytisus*) or non-existent (*Genista*, *Spartocytisus*) outside the plots. In this respect, *Chamaecytisus* might have a slight competitive advantage over *Genista* and *Spartocytisus*, due to the seasonal varying content of alkaloids acting as an herbivore deterrent (Ventura et al., 2000). Due to the large flowering adult individuals found inside the exclosures, seed availability of the three rare shrub species is assumed to be present in their proximity. Herbivores prefer young leaves because of their higher nutrient content and

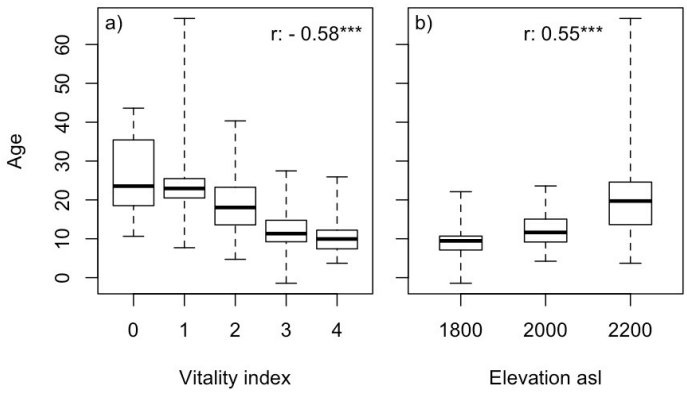

Figure 6. Older *Adenocarpus* individuals are less vital (a), i.e. negatively correlated with age. Mean age of individuals increases with elevation possibly due to higher fire frequency in lower altitudes (b). Correlation is shown as r-values with minus symbols indicating negative correlations.

better digestibility (Coley & Barone, 1996), thus exerting an additional pressure on the few seedlings found outside of the exclosures. Estimations by the National Park suggest that as few as one rabbit per hectare is enough to prevent the seedling establishment of the rare shrubs. In general, the presence of introduced herbivores strongly modifies seedling recruitment in the *codesar*, which is in accordance with the results given by Garzón-Machado et al. (2010) for the *pinar* of La Palma and by Kyncl et al. (2006) for the summit scrub of Tenerife. Then again, the overall higher seed rain of *Adenocarpus* compared to the other species might influence seedling recruitment. This potential bias could not be accounted for in the study, particularly when keeping in mind the large seed quantities needed for successful germination (Palomares Martínez, 1993).

Growth performance of shrub species inside the exclosures after 11 years is not distributed uniformly throughout the subalpine vegetation zone. Western caldera orientations seem to have negative effects on shrub growth performance of *Adenocarpus*, *Chamaecytisus* and *Spartocytisus*, possibly due to leeward drought effects on the west-facing sites or to storm impacts coming from the Atlantic Ocean, whereas *Genista* does not seem to display any preferential growth regarding caldera orientation. Similarly, elevation has a negative impact on the growth of *Adenocarpus*, *Genista* and *Spartocytisus*, with a lowest relative decline of growth height per 100 m elevation in *Genista*. Elevation strongly influences environmental conditions on small spatial scales, especially in mountain environments, among others affecting morphological plant features (Körner et al., 1989). Both findings suggest that *Genista* is actually better adapted to the harsh climatic conditions of the subalpine scrub than other naturally occurring shrub species. In fact, it is presumed to have played a more important role in the past, possibly being the dominant shrub species next to *Adenocarpus* (Garzón-Machado et al., 2011).

Growth heights of *Adenocarpus* measured in exclosure plots are significantly lower than those of the other species, especially those of *Chamaecytisus* and *Genista* (Fig. 4), but also those of *Spartocytisus*, when looking a large individuals only (S2 in supporting information). In the densely covered *codesar* the long-term survival of a shrub individual (no matter which species) is only guaranteed by a successful competition for light. The competitive success is thus at least in parts reflected in growth height of the shrub individuals (Aarssen, 1983). This leads to the conclusion that *Adenocarpus* individuals are less competitive in the absence of herbivores once shrub species have managed to establish. The present mono-dominance is thus proposed to be a direct effect of herbivore pressure.

Age of *Adenocarpus* is positively correlated with elevation. This contradicts the results by González Henríquez et al. (1986), who state that the optimum range of *Adenocarpus* lies between 1500 and 2000 m. Indeed, the oldest individuals and the highest mean age are found in the high-*codesar* (i.e. above 2200 m). This likely reflects the modulating effect of wildfires on the age structure of the *codesar* producing a high abundance of seedlings and saplings and a low abundance of old plants in lower elevations where fire frequencies are highest. However, as previously shown, longevity of shrub species is promoted at high elevations because species tend to grow more slowly causing them to remain in physiologically "younger" state (Diemer, 1998). The data collected in this study can neither conclusively verify nor falsify these hypotheses. Wildfires are a part of the fire-adapted *pinar* ecosystem (Höllermann, 2000; Climent et al.,

2004; Del Arco et al., 2010), which often subsequently spread into the subalpine zone. For example, the last big wildfire event in the subalpine scrub occurred in 2005 destroying large parts of the NW low- and mid-*codesar*, but not spreading into the high-*codesar*. Even though regeneration commenced fairly quickly, no other species besides *Adenocarpus* was observed in the 2005 wildfire area in April 2011 (personal observation).

However, it is not only *Adenocarpus* that is potentially able to create a sufficient soil seed bank inbetween fire events. Other shrub species reach reproduction age as quickly as *Adenocarpus* or even quicker as sowing experiments performed by the National Park Caldera de Taburiente show. Here *Teline* reached the earliest reproduction age after 2-3 years, *Adenocarpus, Chamaecytisus* and *Genista* after 3 years, *Spartocytisus* after 4 years and *Bencomia* after 5 years (Palomares Martínez, 1993). Nevertheless, the other shrub species are caught in a detrimental cycle. Regeneration of non-*Adenocarpus* species only occurs very locally, owing to their comparably heavy seeds that cannot be dispersed over long distances (Palomares Martínez, 1993), i.e. the probability of reaching recently burnt areas or other sites potentially adequate for colonization is low.

We suggest that only the combination of both types of disturbance, introduced herbivores and wildfires, supports the development of mono-dominant *Adenocarpus* stands. As shown in the exclosure plots, regeneration after a fire event would favour non-*Adenocarpus* shrub species (Fig. 3), if a sufficient soil seed bank was available or seeds were introduced from neighbouring and unharmed areas. However, the very low abundance of other shrub species strongly reduces propagule availability and the probability of introduction. Moreover, the selective browsing of herbivores gives the few non-*Adenocarpus* seedlings little chance to reach such a height to where browsing damage is non-lethal. Johansson et al. (2010) showed that the dominance between two shrubby *Erica*-species in an Ethiopian subalpine environment shifted by the presence of grazing cattle and cyclic burning. Analogously, the combination of fire and introduced rabbits greatly reduced vegetation cover, plant biomass and species richness in an Australian subalpine ecosystem (Leigh et al., 1987). However, historic land use practices (e.g. goat herding and cyclic burning) probably left its marks on the current species composition of La Palma's subalpine scrub (see Kyncl et al. (2006) for Tenerife) and the magnitude of this contribution to the legacy of *Adenocarpus* still remains largely unclear.

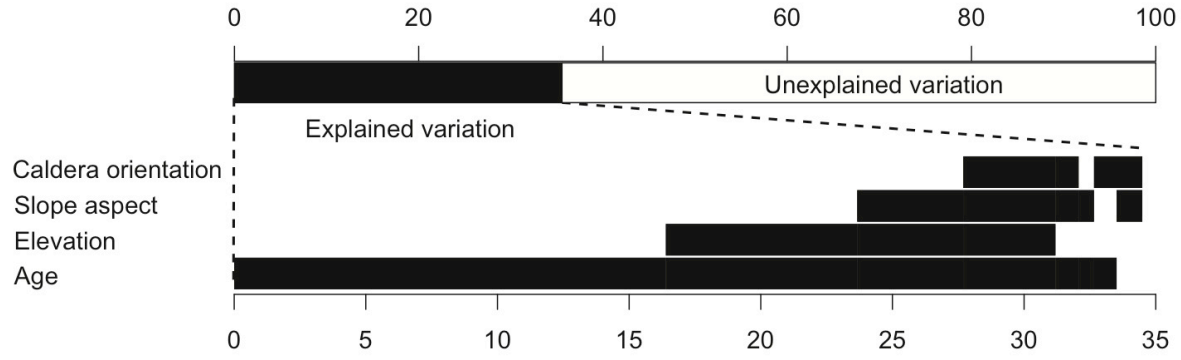

Figure 7. Variance partitioning reveals that vitality of *Adenocarpus* strongly depends on the age of individuals. A differentiation between this effect and elevation or orientation is hardly possible due to a strong overlap in explained variation. The upper bar illustrates the explained variation (black) in comparison with the unexplained variation (white). Within the explained variation the lower bars show how much the specific variables explain independently (i.e. if there is no horizontal overlap between the variable bars) or jointly (i.e. if a horizontal overlap exists between two or more variable bars). For reasons of simplification and improved comprehensibility only contributions of more than 0.5% are displayed.

Life-death pattern in the codesar

Age appears to be the main factor influencing the vitality of *Adenocarpus* individuals. This conclusion is supported by the negative correlation between age and the vitality index (V_i). The variance of age in the old growth plots indicates active rejuvenation following a natural pattern (i.e. natural population dynamic). Wiegand et al. (2000) describe a similar behaviour for two shrub species in the South African semi-arid Karoo. Elevation, as a proxy for climatic gradients, serves as the second master variable that explains the behaviour of the vitality index. Together with slope aspect and caldera orientation microclimatic conditions are strongly modified by elevation (Körner et al., 1989).

In contrast to *Adenocarpus*, both *Genista* and *Spartocytisus* alike show seasonal adaptation to harsh winter conditions by reducing the water content in the terminal branches (Á. Palomares Martínez, unpublished). Therefore, *Adenocarpus* is especially sensitive to the strong northern winds that accumulate ice on the branches (personal observation), thus, theoretically disadvantaging it even more compared to other shrub species. Furthermore, this sensitivity may help to explain the observed life-death pattern in the *codesar*. *Chamaecytisus* and *Teline* seem to show no signs of winter adaptation in their terminal branches (Á. Palomares Martínez, unpublished). Consequently, they are very rare (*Chameacytisus*) or not present at all (*Teline*) in the exclosure sites of the high-*codesar*, even though they were equally sown in all plots.

In summary, the effects of introduced herbivores have a fundamental impact on the interspecific competition and distribution of endemic shrub species in the subalpine zone of La Palma, Canary Islands, and lead one species (i.e. *Adenocarpus viscosus* ssp. *spartioides*) to nearly complete mono-dominance. To implement useful conservation strategies for the protection of the endangered endemic shrub species (i.e. *Bencomia exstipulata*, *Chamaecytisus proliferus* ssp. *proliferus*, *Genista benehoavensis*, *Spartocytisus supranubius* and *Teline stenopetala* ssp. *sericea*) further understanding is needed, in particular, regarding the effects of wildfires and winter ice storms. The impact of introduced herbivores on high-elevation ecosystems of oceanic islands has been largely underrepresented in current and past research. With this case study we hope to have contributed to the gaining of insights on the extent of their impact, possibly leading to future conservation initiatives of endangered endemic species of this and comparable systems.

Acknowledgements

We would like to thank the study program Global Change Ecology (M.Sc.) within the Elite Network of Bavaria for their support, the administration and employees of the National Park Caldera de Taburiente (La Palma) for establishing and maintaining the exclosures during the last 11 years and the anonymous reviewers for their valuable comments and suggestions.

References

Aarssen, L.W. (1983) Ecological combining ability and competitive combining in plants – toward a general evolutionary theory of coexistence in systems of competition. *American Naturalist*, **122**, 707-731

Acebes Ginovés, J.R., León Arencibia, M.C., Rodríguez Navarro, M.L., del Arco Aguilar, M., García Gallo, A., Pérez de Paz, P.L., Rodríguez Delgado, O., Martín Osorio, V. E. & Wildpret de la Torre, W. (2010) *Spermatophyta*. In: *Lista de especies silvestres de Canarias. Hongos, plantas y animales terrestres. 2009*. Arechavaleta, M., Rodríguez, S., Zurita, N. & García, A. (eds.). Gobierno de Canarias, Tenerife, 122-172

Del Arco Aguilar, M.J., González-González, R., Garzón-Marchado, V. & Pizarro-Hernández, B. (2010) Actual and potential natural vegetation on the Canary Islands and its conservation status. *Biodiversity and Conservation*, **19**, 3089–3140.

Bowen, L. & van Vuren, D. (1997) Insular endemic plants lack defenses against herbivores. *Conservation Biology,* **11**, 1249-1254.

Brullo, C., Brullo, S., DeMarco, G., Giusso del Galdo, G. & Guarino, R. (2008) A survey of the orophilous shrubby vegetation of the Teide (Tenerife, Canary Islands). *Feddes Repertorium*, **119**, 63-81.

Bryant, J.P., Provenza, F.D., Pastor, J., Reichardt, P.B., Clausen, T.P. & du Toit, J.T. (1991) Interactions between woody plants and browsing mammals mediated by secondary metabolites. *Annual Review of Ecology, Evolution, and Systematics*, **22**, 431-46.

Cabrera-Rodriguez, F. (2006) Microhabitat selection of the European rabbit on La Palma, Canary Islands, Spain. *Acta Theriologica,* **51**, 435-442.

Cabrera-Rodriguez, F. (2008) Seasonal abundance and management implications for wild rabbits (Oryctolagus cuniculus) on La Palma, Canary Islands, Spain. *Wildlife Biology in Practice*, **2**, 39-47.

Callaway, R.M. & Ridenour, W.M. (2004) Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment*, **2**, 436–443.

Campbell, K. & Donlan, C.J. (2005) Feral goat eradications on islands. *Conservation Biology*, **19**, 1362-1374.

Carracedo, H.C., Pérez Torrado, F.J., Ancochea, E., Meco, J., Hernán, F., Cubas, C.R., Casillas, R., Rodriguez, E. & Ahijado, A. (2002) Cenozoic volcanism II: the Canary Islands. *The Geology of Spain* (ed. by Gibbons, W. and Moreno, T.), pp. 439–472. Geological Society, London.

Caujapé-Castells, J., Tye, A., Crawford, D. J. , Santos-Guerra, A., Sakai, A., Beaver, K., Lobin, W., Florens, F. B. V., Moura, M., Jardim, R., Gómes, I., C. Kueffer. C., (2010) Conservation of oceanic island floras: present and future global challenges. *Perspectives in Plant Ecology, Evolution and Systematics*, **12**, 107-130.

Cheeke, P.R. (1988) Toxicity and metabolism of pyrrolizidine alkaloids. *Journal of Animal Science*, **66**, 2343-2350

Climent, J., Tapias, R., Pardos, J.A. & Gil, L. (2004) Fire adaptations in the Canary Island pine (*Pinus canariensis*). *Plant Ecology,* **171**, 185-196.

Coblentz, B.E. (1978) The effects of feral goats (*Capra hircus*) on island ecosystems. *Biological Conservation,* **13**, 279-286.

Coley, P.D. & Barone, J.A. (1996) Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics*, **27**, 205-335

Courchamp, F., Chapouis, J.L. & Pascual, M. (2003) Mammal invaders on islands: impacts, control and control impact. *Biological Reviews*, **78**, 347-383.

Cushman, J.H., Waller, J.C. & Hoak, D.R. (2010) Shrubs as ecosystem engineers in a coastal dune: influences on plant populations, communities and ecosystems. *Journal of Vegetation Science*, **21**, 821-831.

Darwin, C.R. (1859) *On the origin of species by means of natural selection*. London, John Murray.

Diemer, M. (1998) Life span and dynamics of leaves of herbaceous perennials in high-elevation environments: 'news from the elephant's leg'. *Functional Ecology*, **12**, 413-425

Fernández-Palacios, J.M. & Whittaker, R.J. (2008) The Canaries: an important biogeographical meeting place. *Journal of Biogeography,* **35**, 379-387.

Francisco-Ortega, J., Santos-Guerra, A., Kim, S.C. & Crawford, D.J. (2000) Plant genetic diversity in the Canary Islands: a conservation perspective. *America Journal of Botany*, **87**, 909-917

Garzón-Machado, V., del Arco-Aguilar, M.J. & Pérez-de-Paz, P.L. (2011) A tool set for description and mapping vegetation on protected natural areas: an example from the Canary Islands. *Biodiversity and Conservation*, **20**, 3605-3625

Garzón-Machado, V., González-Mancebo, J.M., Palomares-Martínez, A., Acevedo-Rodríguez, A., Fernández-Palacios, J.M., Del-Arco-Aguilar, M. & Pérez-de-Paz, P.L. (2010) Strong negative effect of alien herbivores on endemic legumes of the Canary pine forest. *Biological Conservation,* **143**, 2685-2694.

González Henríquez, M.N., Rodrigo Pérez, J.D. & Suárez Rodríguez, C. (1986) *Flora y Vegetación del Archipelago Canario*, Edirca, Las Palmas de Gran Canaria.

González, M., Mathieu, A., Augusto, L., Gire, C., Bakker, M.R. & Budynek, A. (2010) Gorse seed bank variability in maritime pine stands. *Seed Science Research*, **20**, 31-38.

Greinwald, R., Bachmann, P., Witte, L., Acebes-Ginovés, J.R. & Czygan, F.C. (1992) Taxonomic significance of alkaloids in the Genus *Adenocarpus* (Fabaceae-Genista). *Biochemical Systematics and Ecology*, **20**, 69-73

Hierro, J.L., Maron, J.L. & Callaway, R.M. (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. *Journal of Ecology*, **93**, 5–15.

Höllermann, P. (2000) The impact of fire on Canarian ecosystems 1983-1998. *Erdkunde,* **54**, 70-75

Hothorn, T., Bretz, F. & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal,* **50**, 346-363.

Irl, S.D.H. & Beierkuhnlein, C. (2011) Distribution of endemic plant species on an oceanic island – a geospatial analysis of La Palma (Canary Islands). *Procedia Environmental Science,* **7**, 170-175.

Johansson, M., Rooke, T., Fetene, M. & Granström, A. (2010) Browser selectivity alters post-fire competition between *Erica arborea* and *E. trimera* in the sub-alpine heathlands of Ethiopia. *Plant Ecology*, **207**, 149-160

Kazakis, G., Ghosn, D., Vogiatzakis, I.N. & Papanastasis, V.P. (2007) Vascular plant diversity and climate change in the alpine zone of the Lefka Ori, Crete. *Biodiversity and Conservation*, **16**, 1603-1615.

Körner, C., Neumayer, M., Palaez Menendez-Reidl, S. & Smeets-Scheel, A. (1989) Functional morphology of mountain plants. *Flora*, **182**, 353-383

Kyncl, T., Suda, J., Wild, J., Wildova, R. & Herben, T. (2006) Population dynamics and clonal growth of Spartocytisus supranubius (Fabaceae), a dominant shrub in the alpine zone of Tenerife, Canary Islands. *Plant Ecology,* **186**, 97-108.

Lausi, D. & Nimis, P.L. (1986) Leaf and canopy adaptations in a high-elevation desert on Tenerife, Canary Islands. *Vegetatio*, **68**, 19-31.

Legendre, P. (2008) Studying beta diversity: ecological variation partitioning by multiple regression and canonical analsysis. Journal of *Plant Ecology*, **1**, 3-8

Leigh, J.H., Wimbush, D.J., Wood, D.H., Holgate, M.D., Slee, A.V., Stanger, M.G. & Forrester, R.I. (1987) Effects of rabbit grazing and fire on a sub-alpine environment .1. Herbaceous and shrubby vegetation. *Australian Journal of Botany*, **35**, 433-464

Leuschner, C. (1996) Timberline and alpine vegetation on the tropical and warmtemperate oceanic islands of the world: Elevation, structure and Floristics. *Vegetatio*, **123**, 193-206.

Lowe, S., Browne, M., Boudjelas, S. & De Poorter, M. (2000) 100 of the world's worst invasive alien species - A selection from the Global Invasive Species Database. *Aliens*, **12**, 1-12

MacArthur, R. & Levins, R. (1967) The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*, **101**, 377–385.

Maher, K.A., Hobbs, R.J. & Yates, C.J. (2010) Woody shrubs and herbivory influence tree encroachment in the sandplain heathlands of southwestern Australia. *Journal of Applied Ecology,* **47**, 441-450.

Navarro, J.F., Martín, E. & Rodríguez, A. (1990) Las primeras etapas del programa de excavaciones en las Cuevas de San Juan y su aportación a las dicronías de la prehistoria de Canarias. *Investigaciones Arqueológicas en Canarias,* **2**, 189–201.

Nezadal, W., Lindacher, R. & Welss, W. (1999) Lokalendemiten und Phytodiversität der westkanarischen Inseln La Palma und La Gomera. *Feddes Repertorium*, **110**, 19-30.

Nogales, M., Rodriguez-Luengo, J.L. & Marrero, P. (2006) Ecological effects and distribution of invasive non-native mammals on the Canary Islands. *Mammal Review,* **36**, 49-65.

Mueller-Dombois, D. & Spatz, G. (1975) The influence of feral goats on the lowland vegetation in Hawaii Volcanoes National Park. *Phytocoenologica,* **3**, 1–29.

Palomares Martínez, Á. (1993) El matorral de alta montaña en la isla de La Palma, seguimiento debido al peligro de extinción de la especie *Genista benehovensis*. In: *Ponencias y comunicaciones. Congreso forestal español - Lourizán*, **2**, 421-425

Palomares Martínez, Á., Méndez Carvajal, C., López Soriano, I. & Delgado Luzardo, A. (2004) *Plan de Conservación del Hábitat de las Cumbres del Norte de La Palma.* Internal document of the National Park Caldera de Taburiente, El Paso, La Palma.

Parkes. J, (1990) Feral goat control in New Zealand. *Biological Conservation*, **54**, 335-348.

Pinheiro, J., Bates, D., DebRoy, S. & Sarkar D (2009) *nlme: Linear and Nonlinear Mixed Effects Models*, R package version 3.1-96.

R Development Core Team (2010) *R: A language and environment for statistical computing. R Foundation for Statistical Computing*, Vienna, Austria, http://www.R-project.org/.

Rafferty, C. & Lamont, B.B. (2007) Selective herbivory by mammals on 19 species planted at two densities. *Acta Oecologia,* **32**, 1-13.

Schütte, H.R., Kelling, K.L., Knöfel, D. & Mothes, K. (1964) Zur Biosynthese von Adenocarpin in *Adenocarpus viscosus*. *Phytochemistry*, **3**, 249-252

Shaben, J. & Myers, J.H. (2010) Relationships between Scotch broom (Cytisus scoparius), soil nutrients, and plant diversity in the Garry oak savannah ecosystem. *Plant Ecology,* **207**, 81-91.

Simberloff, D. (1995) Why do introduced species appear to devastate islands more than mainland areas? *Pacific Science*, **49**, 87-97.

Steinbauer, M. J., Otto, R., Naranjo-Cigala, A., Beierkuhnlein, C. & Fernández-Palacios, J. M. (2011). Increase of island endemism with altitude - speciation processes on oceanic islands. *Ecography*, **34**, 1–10.

Strasberg, D., Rouget, M., Richardson, D.M., Baret, S., Dupont, J. & Cowling, R.M. (2005) An assessment of habitat diversity and transformation on La Réunion Island (Mascarene Islands, Indian Ocean) as a basis for identifying broad-scale conservation priorities. *Biodiversity and Conservation*, **14**, 3015-3032.

Traveset, A., Nogales, M., Alcover, J.A., Delgado, J.D., López-Darias, M., Godoy, D., Igual, J.M. & Bover, P. (2009) A review on the effects of alien rodents in the Balearic (Western Mediterranean Sea) and Canary Islands (Eastern Atlantic Ocean). *Biological Invasions,* **11**, 1653-1670.

Van Vuren, D. & Coblentz, B.E. (1987) Some ecological effects of feral sheep on Santa Cruz Island, California, USA. *Biological Conservation*, **41**, 253-268.

Ventura, M.R., Castanon, J.I.R., Muzquiz, M., Mendez, P. & Flores, M.P. (2000) Influence of alkaloid content on intake of subspecies of *Chamaecytisus proliferus*. *Animal Feed Science and Technology*, **85**, 279-282

Vitousek, P.M., D'Antonio, C.M., Loope, L.L., Rejmánek, M. & Westbrooks, R. (1997) Introduced species: A significant component of human-caused global change. *New Zealand Journal of Ecology,* **21**, 1-16.

Walker, L.R., Clarkson, B.D., Silvester, W.B. & Clarkson, B.R. (2003) Colonization dynamics and facilitative impacts of a nitrogen-fixing shrub in primary succession. *Journal of Vegetation Science*, **14**, 277-290.

Wiegand, T., Milton, S.J., Esler, K.J. & Midgley, G.F. (2000) Live fast, die young: estimating size-age relations and mortality pattern of shrubs species in the semi-arid Karoo, South Africa. *Plant Ecology,* **150**, 115-131.

10. Summary

This thesis includes eight manuscripts with methodological, empirical and theoretical contributions that aim to enhance the understanding of species richness and composition patterns and their underlying drivers. Islands and isolated systems are in the focus of this work.

Islands provide optimal conditions to study biogeographic patterns. Theoretical advances in ecology have been initiated by island biogeography. Theory on island biogeography has particularly been improved by a better representation of time related components including speciation and environmental change. Oceanic islands are not stable systems but follow a characteristic ontogeny. After the volcanic emergence over the sea surface, erosion processes, shaping the island first more heterogeneous and then flatter, transform islands. This thesis shows how particular characteristics of the classic theory of island biogeography can be included in the currently most advanced theoretical framework. While MacArthur & Wilson (1963) particulary focussed on processes (colonisation and extinction) for generating species richness patterns, current theory assumes a defined upper limit for species richness ("carrying capacity"). By reinforcing the importance of processes in the current theory, as suggested in this thesis, it is much simpler to formulate hypothesis that can be tested by empirical data. Carrying capacity is linked to "habitat heterogeneity", both, in the meaning of topographic variability as well as the number of vegetation units that are present in a given area. This thesis demonstrates that a clear terminology is a prerequisite for a profound understanding of the effects of "heterogeneity" on species diversity patterns in general and the underlying biogeographic processes in particular. The heterogeneity of surfaces influences species diversity not only on scales larger than kilometres but also is important on very fine scales of meters and smaller. Novel methods to measure different aspects of surface variability are introduced and discussed and their effect on species richness and composition of plant species groups in different ecological systems is presented.

Furthermore, this thesis highlights the isolating effect of elevation (*elevation-driven ecological isolation hypothesis*). Environmental filtering along an elevational gradient differentiates ecosystems. Isolation increases with elevation, as comparable ecosystems are much farther apart at high elevations than is the case for lowland ecosystems. In addition, ecosystems on neighbouring islands or on the continent that serve as source regions for colonising species are smaller in area in high elevations in comparison to low elevation ecosystems. Consequently, an above average speciation rate reflected in a high percentage of endemic species can be expected for higher elevations on islands and high mountains. The *elevation driven ecological isolation hypothesis* is tested for a number of islands and a new hypothesis indicating a complex interaction with isolation is developed. The difference in isolation between low and high elevation ecosystem diminishes as the overall isolation of the island increases. Thus the relation between the percentage of endemic species and elevation should reverse with an increase in isolation. On very isolated islands, low and high elevation ecosystems are alike isolated but low elevation ecosystems should have an above average speciation rate as they provide more area and higher temperatures relative to the ecosystems above (e.g. metabolic theory of ecology).

The scale dependence of diversity patterns are attributed to ecological processes that operate differently over varying extents and grain sizes. This thesis demonstrates that scale dependencies in distance-decay analyses cannot be traced back to processes that are specific for the ecological scale, but can largely be attributed to sampling design and are highly sensitive to grain size and study extent. Distance-decay analyses are an adequate method to assess spatial turnover in species composition. However, this thesis shows that frequent practise of making comparisons among studies is not possible within the current methodological framework.

Finally, this thesis provides an overview on patterns in species richness and composition and elaborates interconnections between associated theories and underling drivers. Promising novel research questions and directions are identified in the field of island biogeography and in an adequate formalisation of a "heterogeneity" concept.

11. Zusammenfassung

Diese Arbeit umfasst acht Manuskripte mit methodischen, empirischen und theoretischen Beiträgen. Ihr Ziel ist es, das Verständnis von Mustern der Artenvielfalt und Artenzusammensetzungen sowie deren Steuergrößen zu erweitern. Einen Schwerpunkt dieser Arbeit stellen isolierte Systeme mit besonderer Berücksichtigung von Inseln dar.

Inseln bieten optimale Bedingungen für die Untersuchung biogeographischer Muster, was maßgebliche theoretische Fortschritte in der Ökologie durch inselbiogeographische Studien hervorgebracht hat. Aktuelle Verbesserungen der Theorie der Inselbiogeographie erfolgten insbesondere durch die Integration von zeitlichen Aspekten sowie durch die Änderung von Umweltbedingungen. Ozeanische Inseln stellen zeitlich keine stabilen Systeme dar, vielmehr unterliegen wichtige Inselcharakteristika einer Ontogenese. Nach dem Entstehen eines steilen Vulkankegels formen Erosionsprozesse die Topographie der Insel. Über hohe Oberflächenrauigkeit führt dieser Prozess schließlich zu einem flachen weniger komplexen Inselrumpf.

Diese Arbeit zeigt auf, an welcher Stelle die gegenwärtigen theoretischen Überlegungen zur Inselbiogeographie wichtige Aspekte der klassischen Gleichgewichtstheorie vernachlässigen. Während MacArthur & Wilson (1963) auf die Zeit bezogene Prozesse (Einwanderungsrate, Aussterberate) heranzogen um Muster des Artenreichtums zu erklären, fokussieren gegenwärtige Theorien auf eine Obergrenze des Artenreichtums ("Carrying capacity" sensu Whittaker et al. 2008). Eine erneute direkte Integration der biogeographischen Prozesse in die inselbiogeographische Theorie, wie in dieser Arbeit vorgeschlagen, erleichtert das Formulieren präziser Hypothesen und deren Test durch empirische Daten.

Die "Carrying capacity" einer Insel wird über die englischsprachige Bedeutung der "Habitat Heterogenität" sowohl mit topographischer Variabilität als auch mit der Anzahl der Vegetationseinheiten einer definierten Fläche in Verbindung gebracht. Diese Arbeit zeigt, dass eine klare Terminologie eine Voraussetzung für die Untersuchung des Einflusses von Heterogenität auf Muster der Artenvielfalt und die zugrunde liegenden Prozesse bildet. Die Heterogenität von Oberflächen beeinflusst Artenvielfalt nicht nur auf Skalen von Kilometern, sondern ist ebenso bedeutsam auf Skalen von Metern und weniger. Neue Methoden zur Messung verschiedener Aspekte der Oberflächenvariabilität werden eingeführt und diskutiert. Ihre Bedeutung in unterschiedlichen Ökosystemen für Artenvielfalt und Artenzusammensetzung verschiedener Artengruppen wird aufgezeigt.

Darüber hinaus wird in dieser Arbeit eine Änderung der ökologischen Isolation mit der Höhe eingehender betrachtet (*"Elevation-driven Ecological Isolation Hypothesis"*). Entlang von Höhengradienten wechseln sich durch die Veränderung von abiotischen Parametern unterschiedliche Ökosysteme ab. Auf Inseln sind höher gelegene Ökosysteme stärker isoliert als jene der Tieflagen, da vergleichbare Umweltbedingungen für Hochlagen auf dem Kontinent weiter entfernt liegen. Dazu kommt, dass die Fläche von hoch gelegenen Ökosystemen auf dem Kontinent in der Regel weit kleiner ist als die Fläche tiefer gelegener Ökosysteme. Die daraus resultierende stärkere Isolation der höher gelegenen Ökosysteme auf Inseln macht dort eine überdurchschnittliche Artbildungsrate wahrscheinlich. Dies sollte sich in einem höheren Prozentsatz an endemischen Arten in den Hochlagen von Inseln oder hohen Bergen widerspiegeln. Diese Hypothese wird anhand verschiedener Inseln getestet und findet weitgehende Unterstützung. Aus den gewonnenen Erkenntnissen wird eine neue Hypothese abgeleitet, welche eine komplexe Interaktion des Verhältnisses zwischen Endemismus und Höhe mit der Isolation von Inseln aufzeigt. Unterschiede in der Isolation zwischen Hoch- und Tieflagenökosystemen sollten sich mit einer Zunahme der Isolation von Inseln verringern. Folglich dürfte sich auch das Verhältnis zwischen dem Prozentsatz an Endemiten mit der Höhe mit zunehmender Isolation umkehren. Auf sehr isolierten Inseln sind Hoch- und Tieflagenökosysteme vergleichbar stark isoliert. In diesem Fall weisen die Tieflagensysteme eine höhere Artbildungsrate auf, da sie größer und wärmer sind (siehe "Metabolic Theory of Ecology").

Muster der Artenzahl und Zusammensetzung werden auf bestimmten Skalen emergent. Die Ursache dafür wird ökologischen Prozessen zugeschrieben, die auf spezifischen Skalen wirken. Diese Arbeit zeigt allerdings auf, dass eine Skalenabhängigkeit in sogenannten Distance-decay-Analysen nicht ausschließlich auf skalenabhängige Prozesse zurückgeführt werden kann. Vielmehr beeinflusst das Aufnahmedesign (Körnung der Aufnahmen und Ausdehnung des Untersuchungsgebietes) maßgeblich das Ergebnis. Distance-decay-Analysen werden herangezogen um Änderungen in der Artzusammensetzung mit der Entfernung zu quantifizieren. Die vorliegende Arbeit zeigt, dass die gängige Praxis eines Vergleiches zwischen verschiedenen Untersuchungen mit diesem gegenwärtig gebräuchlichen Verfahren methodisch inhärenten Einschränkungen unterliegt.

Diese Arbeit bietet einen Überblick über grundsätzliche Muster der Artenvielfalt und Artenzusammensetzung. Sie erarbeitet Verbindungen zwischen verschiedenen Theorien und zugrunde liegenden Steuergrößen. Vielversprechende neue Forschungsfragen ergeben sich auf dem Gebiet der Inselbiogeographie und über eine adäquate Formalisierung eines Heterogenitätskonzeptes.

Hiermit erkläre ich, dass ich die vorliegende Dissertationsschrift selbständig verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Hiermit erkläre ich, dass ich weder die vorliegende noch eine gleichartige Doktorprüfung an einer anderen Hochschule endgültig nicht bestanden habe.

(gez. Manuel Steinbauer)